

AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024
Number 2965, 45 pp., 12 figs., 3 tables February 27, 1990

Oligo-Miocene Vertebrates from Puerto Rico, with a Catalog of Localities

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ABSTRACT

Vertebrates from Oligocene and Miocene localities in northern Puerto Rico are described. Two vertebrae—one of a probable boid and one of a possible iguanid—from fluvial/nearshore facies of the Miocene Cibao Formation are the first specimens of land vertebrates to be recovered from Tertiary sediments on this island. Other finds, mainly from the Miranda Sand Member of the Cibao Formation, include chelonians, crocodilians, and sirenians (the last including one probably new species, and another provisionally identified as the New World dugongid *Metaxytherium cal-*

vertense). Fossil vertebrates from the extensive paleontological collection of Narciso Rabell Cabrero, briefly described here, include chelonians, crocodilians, selachians, and numerous sirenian remains partly attributable to the San Sebastian (Late Oligocene) dugongid *Caribosiren turneri*.

Although paleontological prospecting for Tertiary vertebrates in Puerto Rico began in the early years of this century, no analytical catalog of localities has been published heretofore. The catalog included in this paper selectively emphasizes mammals and reptiles.

INTRODUCTION

This paper has three objectives. The first is to present descriptions and analyses of the Tertiary vertebrates collected by the authors in Puerto Rico in 1987 and 1988. Recent years have witnessed a rejuvenation of interest in Caribbean biogeography, partly gen-

erated by Rosen's (1975, 1978, 1985) controversial vicariance model of the faunal history of the West Indies (e.g., see Baker and Genoways, 1978; Pregill, 1981a; Savage, 1982; Buskirk, 1985; Guyer and Savage, 1986; Kluge, 1988; Williams, 1989). The purpose

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of our expeditions was to search for the kinds of biological evidence—fossils of Tertiary land vertebrates—that we believe may eventually prove to be critical for the competitive testing of biogeographical scenarios. We are pleased to be able to report a definite if limited success in this endeavor, the recovery of single vertebral elements provisionally referred to Boidae and Iguanidae, from a locality in the Early Miocene Cibao Fm in the northwestern part of the island. These finds constitute the first discovery of land amniotes in an undoubtedly Tertiary context in Puerto Rico.

The second objective is to provide information on the contents of an important collection of vertebrate fossils amassed by Narciso Rabell Cabrero and donated by his family to the American Museum of Natural History in 1987. This collection includes remains of some apparently new sirenians and chelonians that will be the subject of more detailed reports by other workers.

The last objective is to present a catalog of Tertiary vertebrate localities and the fossils found at them. This catalog is purposely biased toward sites which have yielded mammals, which constitute our special interest. Although the locality list is not impressive in length, it serves to indicate where collecting activities might be focused in the future.

ABBREVIATIONS

Institutional

AMNH-HI	Department of Herpetology and Ichthyology, American Museum of Natural History
AMNH-M	Department of Mammalogy, American Museum of Natural History
AMNH-VP	Department of Vertebrate Paleontology, American Museum of Natural History
USNM-NH	Division of Paleobiology, United States National Museum of Natural History

Anatomical and Stratigraphical

c	centrum
con	condyle
cot	cotyle
Fm	formation (formally named)
ft	foramen transversarium
Lm	limestone (as part of a formal name)

Mbr	member (formally named)
MS	Miranda Sand Mbr, Cibao Fm
nc	neural canal
ns	neural spine
ob1	first (lower) oyster bed at AMNH loc. PR 87-4
ob2	second (upper) oyster bed at AMNH loc. PR 87-4
poz	postzygapophysis
prz	prezygapophysis
QA	Quebrada Arenas Mbr, Cibao Fm
syn	synapophysis
za	zygantrum
zo	zygosphen

ACKNOWLEDGMENTS

Our project had its genesis in inspirational discussions with Malcolm C. McKenna and the late Donn E. Rosen (AMNH). We are grateful for their encouragement. Daryl Domning (Howard University), David Grimaldi (AMNH), Max Hecht (City University of New York), Malcolm C. McKenna (AMNH), Peter Meylan (University of South Florida), Mort Turner (University of Maine), and Ernest Williams (Harvard University) freely shared their expertise and ideas with us. As always, Lorraine Meeker, Chester Tarka, and Jeanne Kelly (AMNH) were unflagging in their help and advice with illustrations and specimen preparation. We thank Daryl Domning, Max Hecht, Veronica MacPhee, Malcolm McKenna, Gregory Pregill, and John Van Couvering for reading and criticizing this paper.

We are grateful to Barbara Citrón and Eduardo Cardona of the Departamento de Recursos Naturales in San Juan for helping us to obtain collecting permits. We are additionally indebted to Barbara for arranging our initial meeting with Dr. Gualberto Rabell. In Puerto Rico, we received assistance from Janice Voltzow, Ned Fetcher, Richard Thomas, and Manuel Vélez (all of the Departamento de Biología, Universidad de Puerto Rico, Río Piedras). We are especially grateful to Janice and Ned for accommodation while in San Juan. The Joaquín González family of Vega Alta graciously allowed us to excavate on their property (AMNH loc. PR 87-4). Our fieldwork in Puerto Rico was made possible by grants from the Philip McKenna Foundation and Duke University.

FAUNAL HISTORY AND BIOGEOGRAPHY OF THE CARIBBEAN

Most of the islands constituting the West Indies³ are oceanic in the geographical sense, meaning that they are currently separated from nearby continents by significant water gaps, benthic deeps, or both. Yet virtually all of them have, or very recently had, terrestrial amniotes in their faunas (Olson, 1978; Morgan and Woods, 1986). The identification of the mechanism(s) that permitted terrestrial amniotes to occupy the land masses of the West Indies continues to be a subject of debate in historical biogeography. Three kinds of explanations have been proposed. (1) Ancestors might have traveled across land-bridges stretching from the American mainland to the islands. Species distributions were thereafter delimited by seaways resulting from land-bridge subsidence or rising sea levels. (2) Ancestors might have dispersed from their centers of origin by rafting, hurricane transport, or other exceptional means. Species distributions are therefore the product of accumulated accidents. (3) Ancestors might have occupied the Antilles soon after the islands' origin/emergence close to or contiguous with surrounding continents. Species distributions were subsequently controlled vicariantly by, *inter alia*, the subdivision, rotation, collision, and/or lateral translation of landmasses under the pervasive influence of plate motions and other tectonic phenomena. The land-bridge argument, an early favorite (Spencer, 1895; Schuchert, 1935), suffers from an acute lack of supporting geological fact and is no longer considered a contender. The other two hypotheses have their ardent sup-

porters, and there is, in consequence, an extensive literature devoted to the disputations of these camps (recently summarized by Williams, 1989). Our purpose here is not to provide additional summaries, but instead to point out how paleontological investigations may help to supply an evidentiary basis for competitively testing dispersion and vicariance in the West Indian context, with particular reference to the Greater Antilles.

One of the clearest and potentially testable differences between dispersionism and vicariance concerns contrasting expectations about the nature of faunal change in the Caribbean as it might be reflected in a good paleontological record. These expectations are reflected in the following quotations from works by Darlington (who accepted the primacy of dispersion) and Rosen (who rejected it):

[I]f the fauna of the Greater Antilles were the residue of a larger fauna of continental type, the present characteristics of the fauna might have arisen by extinction of animals unfitted for, and survival and multiplication of animals fitted for life on islands. There are, however, several objections to this . . . It appears, then, for various reasons, that the faunal peculiarities of the Greater Antilles are not the result of large-scale elimination of animals unsuited to island life. (Darlington, 1938: 293)

One other important way that fossils may serve biogeography is . . . by illustrating substantial extinctions (65 species of mammalian fossils are recorded from the West Indies alone) . . . [that] can represent only a fraction of all extinctions. (Rosen, 1975: 458)

If colonization of the islands of the West Indies by terrestrial amniotes was sporadic and fortuitous, as all truly dispersionist models contend, then there is no reason to suspect that a transect through (for example) the Miocene terrestrial fauna of Cuba would be any richer or more "balanced" than its animal life is known to have been during the Quaternary (fig. 1). Indeed, if there have only been accumulations, then the taxa in that transect ought to be restricted to those lineages that are represented in Pleistocene and Holocene localities. Not all lineages need be represented in this particular transect if some introductions were post-Miocene, but *numerous* additional taxa (*i.e.*, ones with no Quaternary representatives) would be unex-

³ There is much definitional flaccidity in the terms "Antilles," "West Indies," "insular Neotropics," and "islands of the Caribbean Sea." Whether any useful temporal, as opposed to geographical, rigor can be applied to these terms is open to debate. For example, the most rigorous form of definition would have to be based on the historical "cladogram" of "unit" land masses, the origin and vicissitudes of which are barely understood at present. The cladistic metaphor may be inapplicable if, as is likely, some landmasses have had a complicated history of amalgamation as well as subdivision (*cf.* Kluge, 1988).

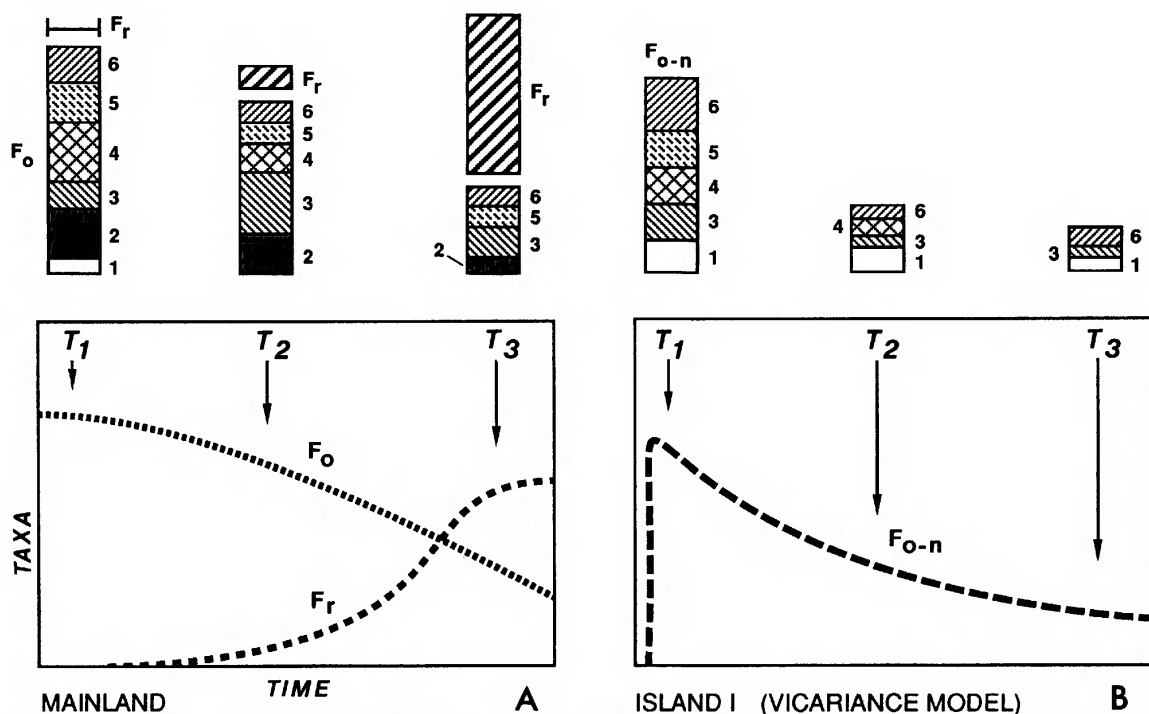


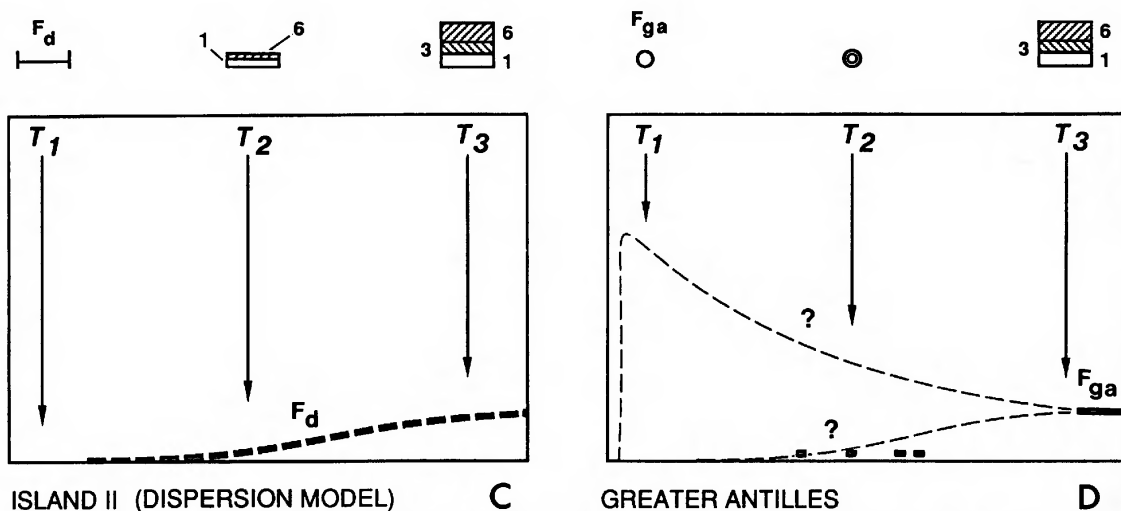
Fig. 1. Assumed vicariance and dispersion scenarios for an imaginary continent (A) and two islands (B, C), compared to existing knowledge of the faunal history of Greater Antilles (D). On the graphs, "TAXA" is a measure of faunal diversity (number of higher-level taxa); "TIME" is some geologically long period. T1, T2, and T3 are specific sampling points within the temporal continuum; faunal composition at each sampling point is shown in the superjacent histogram (relative abundance of individual taxa indicated by size of each shaded area).

A, Mainland. At T1, the original fauna of the Mainland (F_o) consists of 6 higher-level taxa, as depicted in histogram. Over time, Mainland's original fauna declines in diversity (taxa 1 and 4 become completely extinct, while taxon 2 is severely reduced by T3). This reduction is offset by in-migration of new taxa (F_r) from elsewhere; thus net diversity remains high, as is typical of continental faunas.

B, Island I (vicariance scenario). Immediately prior to T1, tectonic processes create Island I. Among possible mechanisms of island formation are rifting and drifting of a continental fragment, or appearance of an island-arc adjacent to or actually overlapping Mainland. With rifting, subdivision of land would produce a simultaneous subdivision of preexisting F_o fauna; with island-arc formation, F_o fauna would have to cross a temporary landbridge or minimal seaway in order to occupy the new land. Only the first mechanism meets a rigorous definition of vicariance; but the second would mimic the results of true vicariance if the crossing from the mainland to the island were exceptionally easy for most faunal elements. Either way, the fauna of Island I may be represented as F_{o-n} , where n represents the small number of Mainland taxa that either did not inhabit the area in which rifting occurred, or did not make the easy land- or water-crossing. Between T1 and T3, the island's fauna rapidly diminishes in diversity because of high differential extinction rates. Unlike the Mainland parent fauna—which is replenished by F_r immigrants during this time interval—the island's fauna gains no new members except through in situ radiation of stocks already present (colonization is prevented because either drifting widens island/mainland gap, or landbridge disappears).

C, Island II (dispersion scenario). Unlike Island I, Island II was never continuous with or geographically close to Mainland. A terrestrial fauna is lacking at T1 (and all earlier times); all faunal emplacements that occur after T1 are due to dispersion across a persistent and wide water barrier. The net rate of increase in taxa (due to in situ evolution or continuing immigration) is shown as exceeding the net rate of decrease (due to extinction); thus the graph for this dispersion-created fauna (F_d) slopes gently upward across time.

By T3, the faunal diversity of Islands I and II has converged toward identity (T3 histograms), even though their faunal histories are dramatically different. In the vicariance scenario, faunal diversity sinks



between T1 and T3, due to the complete loss of all species representing taxa 5 and 4. By contrast, in the dispersion scenario, the number of higher-level taxa rises from zero at T1 to three at T3. Taxa 5 and 4 were never members of this latter fauna. F_r elements from the later continental fauna might also be expected to appear on an island in a dispersion scenario, although none is indicated in this particular example. In a vicariance scenario, F_r elements would be unexpected since they postdate faunal subdivision prior to T1.

D, Greater Antilles. The known Quaternary fauna of the Greater Antilles (F_{ga}) is indicated by the solid line; pre-Quaternary fossils are indicated by isolated data points. As is obvious, direct evidence bearing on the pre-Quaternary diversity of land vertebrates in the Greater Antilles is essentially non-existent. The handful of fossil discoveries made to date do not provide an adequate framework for determining whether vicariance or dispersion was the predominant mode of faunal assembly on these islands—hence the question marks above the outline graphs. It remains to be seen whether the thinness of the existing record is real (failure to recover significant pre-Quaternary terrestrial faunas is due to their actual absence) or artifactual (failure is due to inadequate prospecting efforts).

pected. Naturally, given the length of time between the Miocene and the present, some species turnover is likely to have occurred, but if dispersion is exclusively responsible for the formation of terrestrial amniote faunas in the Caribbean, one would not expect to find a *markedly different* or *systematically more diverse* faunal assemblage at any time in the past.

By contrast, if whole biotas corporately moved onto the proto-Antilles or any subset thereof, as Rosen (1975) contemplated, then there is every reason to suspect that the Quaternary faunal assemblages of the islands are “depauperate” in the full sense of the term

(i.e., “made poor,” as from a prior condition of wealth). Depending on extinction schedules following the vicariant event(s), the same Miocene transect ought to reveal a much larger and more diverse fauna than exists today or has existed in the recent past (fig. 1). Given a specific time of onset for a presumed vicariant event, it should be potentially possible to show, via the recovery of fossils, that the kinds of taxa represented actually reflect the contents of some coeval, continental fauna. “Reflect” need not mean faunal isomorphy, taxon for taxon, between island and continent. Assuming that species/area relationships for existing island faunas are applicable

to ancient ones (cf. Diamond, 1984; Case, 1989), even if near-isomorphy existed shortly after the vicariant event, high subsequent extinction rates would rapidly affect the degree of faunal resemblance. Nevertheless, if a vicariant event affecting a large number of organisms actually occurred, that fact should be registered in a sufficiently early transect in the form of *numerous* now-extinct taxa *in addition to* the ancestors of the lineages that survived into the Quaternary. This formulation may be seen as a restatement, from a paleontological perspective, of Kluge's (1988: 316) emphasis on the "syn-taxon" as the appropriate unit of evidence for analyzing biotic history. ("A syn-taxon is a composite of sister lineages which occupy two or more different areas of endemism.")

The italicized words in the preceding paragraphs are meant to call attention to the point that the paleontological discovery of a few Tertiary taxa with no Caribbean Quaternary representatives would not be dispositive one way or the other for the biotic history of the West Indies. For example, Williams (1989) is completely justified in stating that the recovery of several small terrestrial amniotes—all apparently members of still-extant Antillean genera—in Tertiary Dominican ambers (see below) is interesting but insufficient as conclusive evidence for vertebrate vicariance (see also Mayer and Lazell, 1988). From Williams' (1989) perspective, the value of isolated finds for selecting between dispersion and vicariance is meagre at best, because a handful of taxa do not supply decisive evidence for the prior existence of a more extensive Tertiary biota. We agree. Nevertheless, the promising thing about these discoveries is that faunal turnover in at least some taxa may have been slow enough to permit the expectation that evidence for vicariance—if it exists at all—is potentially recoverable with diligent effort. A paleontological research program is the only one which is capable of supplying positive evidence of "missing taxa" (i.e., taxa whose presence on a landmass is a prediction from or a necessary correlate of some analysis, but physical evidence of which is lacking). The significance of "missing taxa" in biogeographical analysis has been discussed by several authors (e.g., Nelson and Platnick, 1981; Kluge, 1988).

Kluge (1988: 318) has recently stated that "A missing taxon is equivocal because it can't be decided with the information available whether the missing taxon was never present or merely unsampled (alive or extinct)." But the equivocacy is always potentially resolvable, and is fully and positively resolved once fossils (or unsampled extant populations) of the taxon in question are discovered.

Incidentally, it should be noted that island-island vicariance events are only slightly less interesting than continent-island events, even though they severely complicate the interpretation of taxon/area cladograms (Kluge, 1988). Island-island vicariance affecting terrestrial vertebrate taxa may well have occurred during the evolution of Cuba, Hispaniola, and Puerto Rico. The majority of recent tectonic reconstructions of the Caribbean have inferred that these islands are composed of suites of tectonic slivers, progressively amalgamated as a result of movement along a series of major fault systems during the early Cenozoic (illustrated and discussed by Ross and Scotese, 1988; Pindell et al., 1988; for an early recognition of this style of origin for Puerto Rico, see Turner, 1972). Ross and Scotese (1988) suggested that the slivers contributing to northern Hispaniola and to Puerto Rico were in association until approximately 36–21 Ma, when they pulled apart. It is now certain that terrestrial vertebrates were in northern Hispaniola and Puerto Rico by the end of this period (Early Miocene). A vicariance argument would assume that there was complete or nearly-complete faunal isomorphy across the structural units of Hispaniola/Puerto Rico at this time. Faunal resemblance as measured by species identity should have progressively *decreased* after the decoupling of the blocks making up the definitive islands, as a result of differential extinction, divergent evolution, and, of course, the absence of any faunal replenishment by dispersion. By contrast, a dispersionist argument would assume that, whatever the tectonic picture, there was no single forcing function lying behind the immigration events that took place: some species reached one island, some the other, with no causal connection inter se. Interisland transfers are required to explain between-island faunal similarities, but these transfers would

have been serendipitous and presumably would not have affected all species (or even a majority). They also would have taken time, in which case the only possible conclusion is that the faunal similarity of these islands should have *increased* as a function of time. (This is the simplest contrast; it is possible to specify others, most of which converge on the vicariance scenario, making it difficult to imagine tests or bodies of data that would permit discrimination between vicariance and dispersion.)

To the potential objection that existing tectonic reconstructions have already shown that continent-island vicariance is out of the question for "late-evolving" amniotes (e.g., Cenozoic eutherian families) because their phyletic differentiation occurred after plate motions had already carried the units comprising the proto-Antilles far into the Caribbean Sea, we would simply draw attention to the fact that modellers have yet to achieve consensus on many of the matters that are critical to the use of tectonic information for resolving faunal history (see Williams, 1989; Perfit and Williams, 1989). Numerous competing models are now on offer (Burke et al., 1984; Smith, 1985), and by selectively shopping one can find at least one model to fit practically any biogeographical thesis. Donnelly's (1985) reconstruction, for example, implies that the Greater Antilles have always been in essentially their current positions and have experienced minimal motions. At the other end of the spectrum, Sykes et al. (1982) presented a paleogeography of the Caribbean at 38 Ma that positions Jamaica and South Hispaniola adjacent to the Central American coast and the other islands (Cuba, North Hispaniola, and Puerto Rico) in a tightly packed cluster off Yucatán. If Donnelly's model is correct, the probability that vicariance is an explanation for the presence of land mammals in the West Indies is vanishingly small. Conversely, if Sykes et al. (1982) are correct, vicariance cannot be reasonably excluded from consideration.

Another important point is that tectonic reconstructions are basically concerned with megascale events. As Williams (1989) incisively pointed out, many of the events of greatest interest to biogeographers occur at microscale levels, either temporally or geo-

logically, and these are among the kinds of events that are least amenable to reconstruction. Where, exactly, did the island arc (or arcs) that formed the core of the proto-Antilles arise? When, precisely, did subaerial landmasses appear in what is now the Caribbean Sea? Did these landmasses ever form dry land contacts with North or South America (or both), and, if so, specifically when and for how long? To a greater or lesser degree, the geological evidence currently available provides nothing close to the level of resolution needed to answer any of these questions. At present, therefore, we lack the evidentiary basis for accepting any tectonic reconstruction as definitive (Smith, 1985). Barring some methodological breakthrough, we have to accept that we may never have a tectonic reconstruction with a grain fine enough to employ as a standard for determining the comparative likelihood of vicariance vs. dispersion in any given instance (Perfit and Williams, 1989). For this reason, biological—particularly paleobiological—evidence continues to be more significant than geological evidence for interpreting the faunal history of the Caribbean.

MIDDLE TERTIARY GEOLOGY OF PUERTO RICO

The terrestrial geology of Puerto Rico is comparatively well investigated. Monroe (1980) has comprehensively summarized the literature on the middle Tertiary of the island, and our coverage of this topic will therefore be brief and selective. Information on the geology and age of specific formations is presented in the relevant sections of the catalog. Formal names and durations of epochal and subepochal units generally conform to those recommended by Berggren et al. (1985); "early," "middle" (or "medial"), and "late" as informal temporal terms are not capitalized.

Puerto Rico (8897 km²) is the easternmost member of the Greater Antilles, which are in turn the subaerial parts of the Greater Antilles Ridge (Garrison et al., 1972). Puerto Rico is the major island on the Greater Puerto Rican Shelf, a shallowly submerged (<200 m sill depth) platform extending from Puerto Rico to Anegada, a distance of

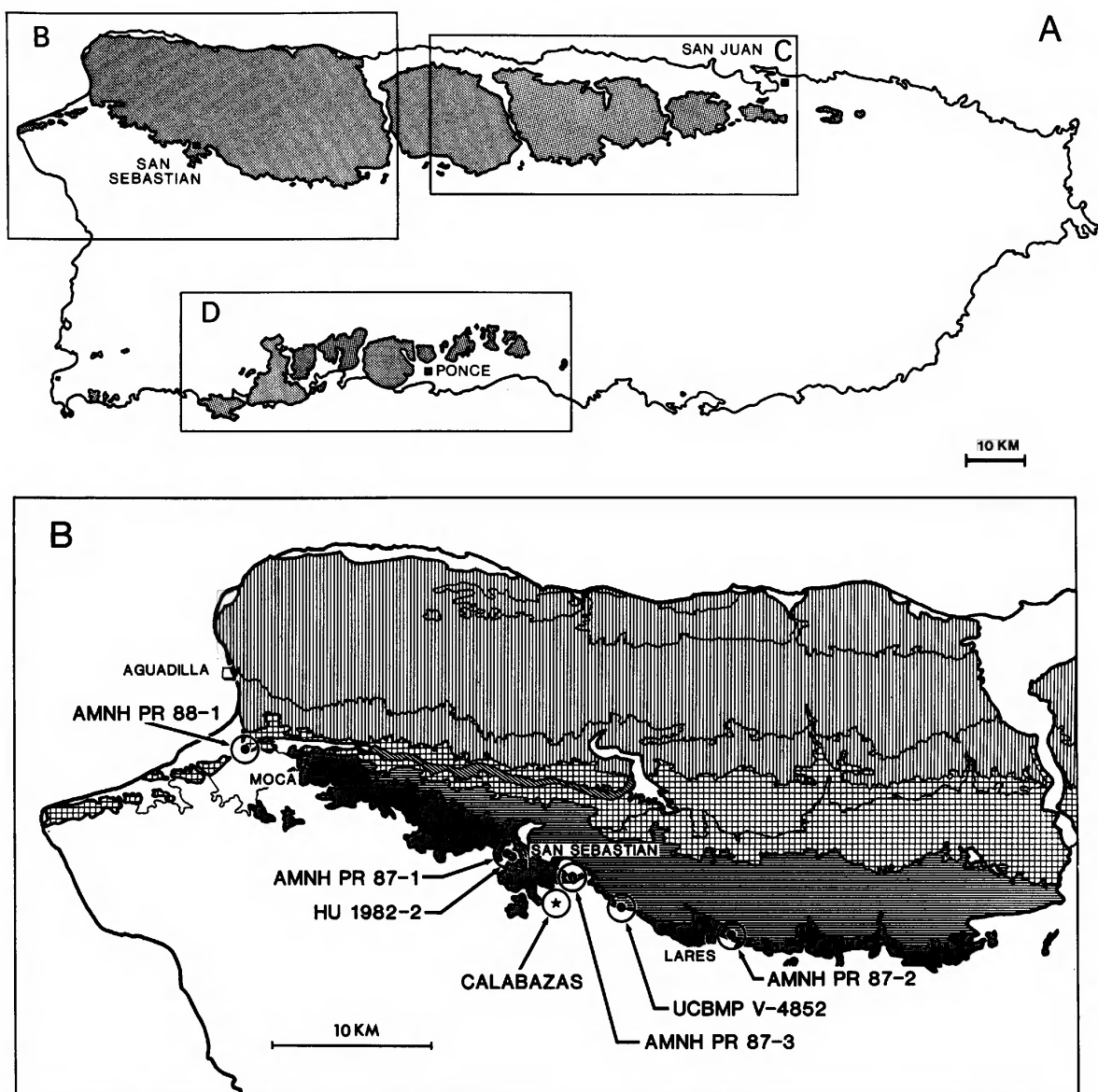
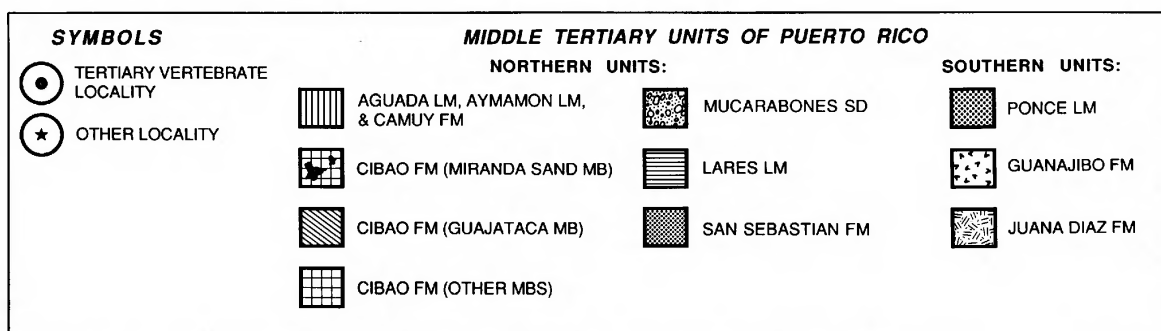
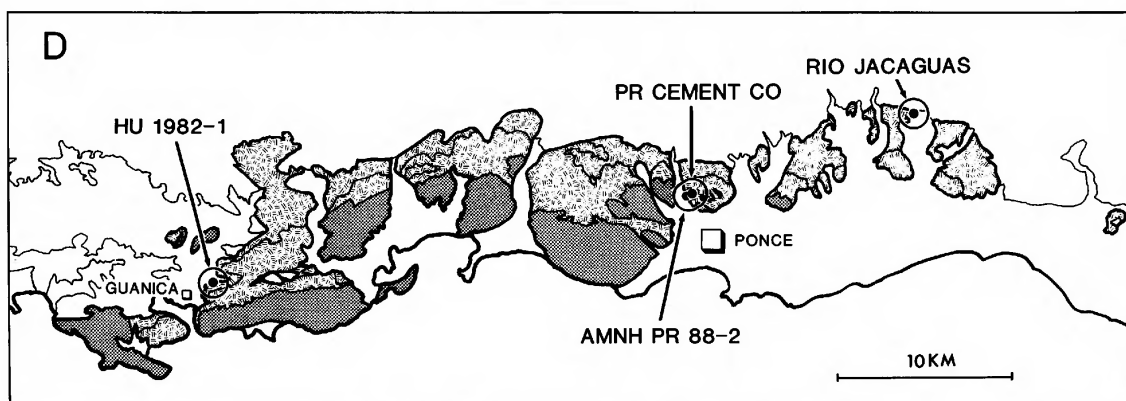
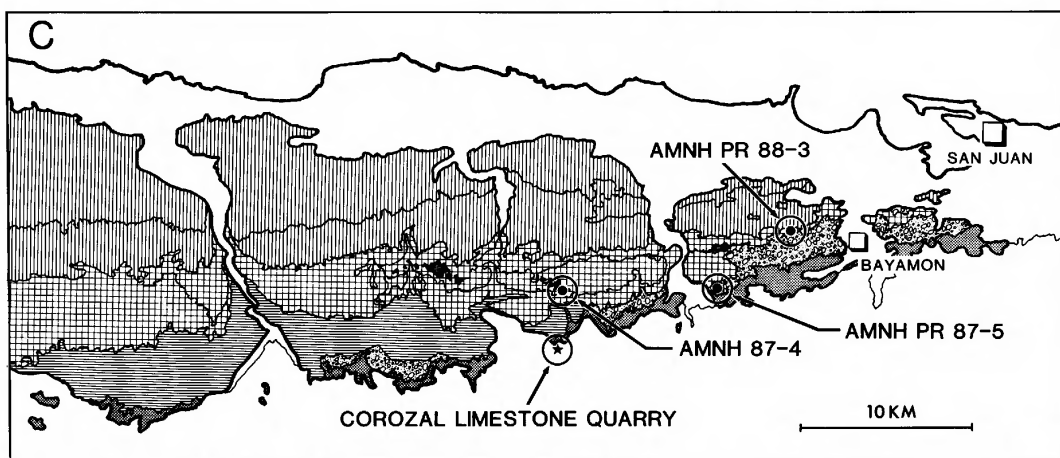


Fig. 2. Middle Tertiary geological formations of Puerto Rico (after Monroe, 1980) and positions of vertebrate localities discussed in text: A, outline map of Puerto Rico; B-D, enlargements of areas in boxes in A. The Carbonate Province (shaded areas) consists of northern and southern sections separated by the Cordillera Central Province. The Coastal Lowlands Province (unshaded) consists of Pleistocene deposits concentrated along the littoral and within the gorges of the large rivers that crosscut the Carbonate Province (MB = Member; SD = Sand).

some 250 km. This shelf is bounded on all sides by significant deeps: the Puerto Rico Trench (−9220 m greatest depth [gd] below sea level), Muertos Trough (−5048 m gd), Virgin Islands Trough (−4506 m gd), and Mona Canyon (−4562 m gd).

Puerto Rico (figs. 2, 3) is divisible into three geological provinces that crosscut the island

in striplike fashion. The Cordillera Central Province consists of moderately deformed igneous and sedimentary rocks of the Older Complex (Cretaceous to Eocene in age), with associated ultramafic and plutonic intrusions. The northern and southern sections of the Coastal Lowlands Province consist of floodplains, marsh deposits, eolianites, and



beach and dune deposits of approximately Pleistocene age. Neither of these provinces has yielded pre-Quaternary fossil vertebrates and need not be considered further here.

Between the cordillera and coastal provinces on either side of the island is the Carbonate Province, divided into northern and southern sections. These consist of compar-

atively narrow belts of limestones, shales, and sands of Early Oligocene through Pliocene age (Bermúdez and Seiglie, 1970; Seiglie and Moussa, 1984; Moussa et al., 1987). The northern carbonate sequence has a maximum width of about 25 km; it is relatively undeformed and dips gently seaward. The southern sequence, less than 10 km wide at its

MIDDLE TERTIARY LITHOSTRATIGRAPHIC UNITS OF PUERTO RICO

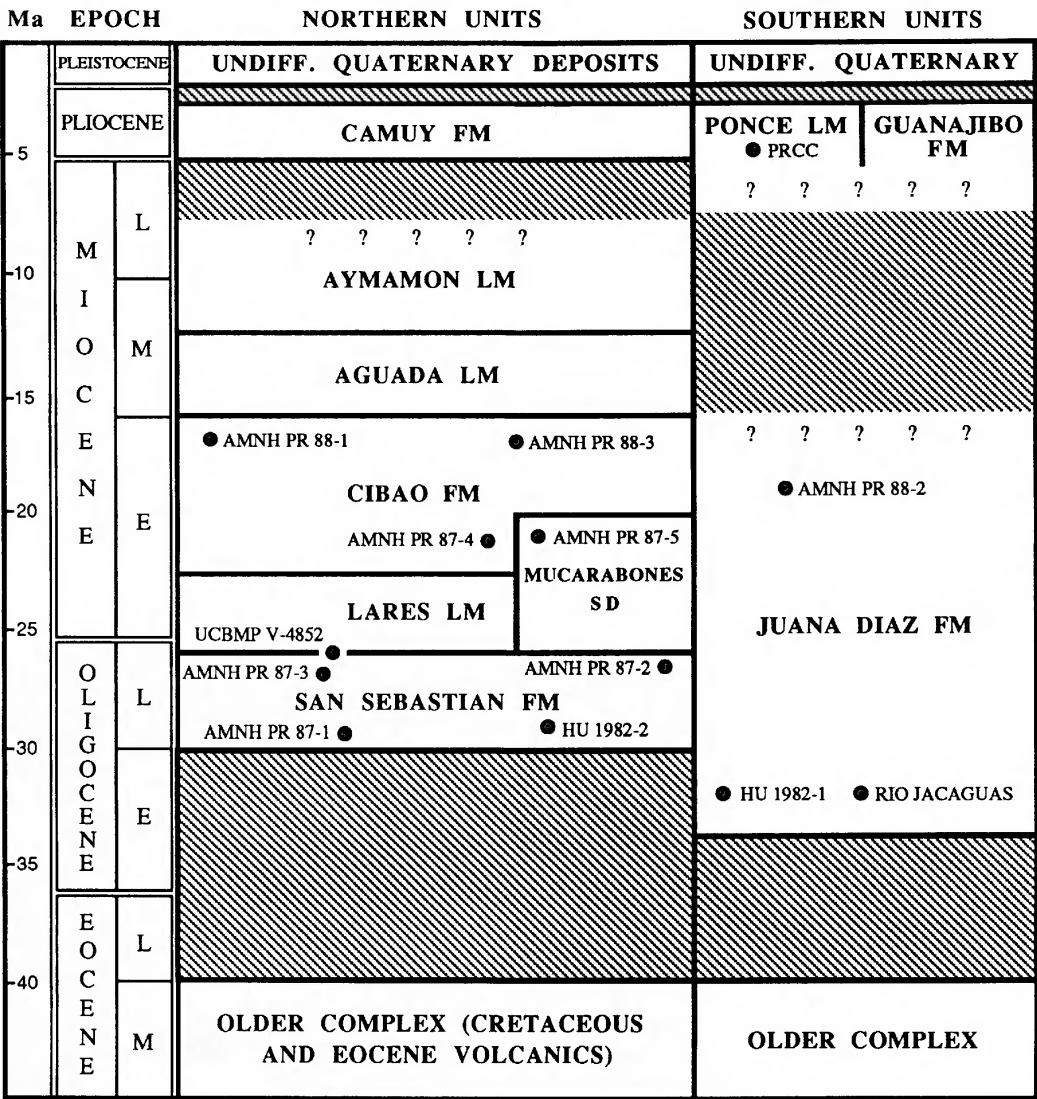


Fig. 3. Columnar section of middle Tertiary lithostratigraphic units of Puerto Rico, largely based on Monroe (1976, 1980). Shaded areas indicate major unconformities. Approximate temporal positions of the localities discussed in text are also indicated. Monroe (1980) used a threefold division of the Oligocene, but a twofold subdivision (Rupelian/Lower and Chattian/Upper) with a stage boundary at approximately 30 Ma is now generally recognized (Berggren et al., 1985).

maximum, consists of discontinuous blocks of carbonates which have been much affected by tectonic movements. Cretaceous and early Tertiary rocks widely separate rocks of these two sequences along both the eastern and western coasts, and no mid-Tertiary units span the central part of the island (although there is some limited evidence for a connection between the northern and southern de-

positional basins along the west coast, at an uncertain time during the Miocene [Monroe, 1980]). Because elements of the northern and southern sequences have distinct invertebrate assemblages with few stratigraphically correlatable species in common, it has proven difficult to link units suspected on lithological grounds to be of similar age. However, the sequences are thought to be roughly time-

equivalent (fig. 3), with the proviso that the oldest Neogene carbonates in the south appear to be slightly older than the oldest in the north (Moussa and Seiglie, 1970).

Mattson (1984) theorized that major changes in plate arrangement and motion in the West Indian region are reflected in a series of pan-Caribbean geologic discontinuities (mainly major unconformities) approximately dated to 110, 85, 66, 45, and 27 Ma. (In some cases these dates do not precisely correspond with epochal divisions in the time scale of Berggren et al. [1985].) For the Greater Antilles, the periods of time bracketed by these discontinuities can be characterized as relatively discrete rock-forming intervals. Three of these intervals cover the Cenozoic. The first period, 66–45 Ma (Paleocene–Middle Eocene), was a time of island-arc volcanism, clastic and epiclastic sedimentation, and deformation. In Puerto Rico, this phase continued into the Early Eocene, at which time volcanic activity and large-scale orogeny abruptly terminated. The end of this period is marked by a profound unconformity which separates rocks of the Older Complex from those of Early and Late Oligocene age (Juana Diaz Fm in the south, San Sebastian Fm in the north). This unconformity appears to represent an erosion interval that occurred between the Middle Eocene and the medial part of the Oligocene, one which witnessed the original appearance of ancestral Puerto Rico as a subaerial land mass (Monroe, 1980). In this context it is useful to note that the existence of an emergent ancestral Puerto Rico during the Oligocene is independently substantiated by excellent palynological evidence for a diversified upland and lowland flora during San Sebastian time (Graham and Jarzen, 1969).

The second period, 45–27 Ma (Late Eocene–Late Oligocene), was a phase of uplift, erosion, and deposition of clastic and carbonate rocks throughout the Greater Antilles. During Oligocene time orogenic movements considerably increased the net elevation of ancestral Puerto Rico, but much of the island's subaerial relief was thereafter reduced by erosion. Near the Oligo-Miocene boundary (27–25 Ma) there was a marine transgression in Cuba and Jamaica; the Jamaican one may have involved the nearly complete sub-

mergence of the island (Arden, 1975; Buskirk, 1985). Mattson (1984: 144) noted that there is no major break in the northern Puerto Rican sequence around 27 Ma, although there was "a change in deposition in the Late Oligocene or Early Miocene from dominantly clastic sediments with subordinate marls and limestones to dominantly limestone with calcarenite and marls." This presumably refers to lithological changes seen in the northern sequence between the upper San Sebastian through to the end of the Lares deposition.

The last period, 27–0 Ma (late Tertiary and Quaternary), was a phase of uplift, erosion, and tilting. In Puerto Rico, the early and middle portions of this time range are classified as times of carbonate deposition, when few clastics were being deposited. There was, however, at least one phase of uplift, subsidence, and renewed uplift in Middle to Late Miocene time. The subsidence, registered in the nearly pure Aymamon Limestone (mostly Late Miocene), is of some importance because the land area of Puerto Rico was probably significantly diminished at this time. The unconformable contact between the uppermost Aymamon and overlying Camuy Fm (partly equivalent to the Quebradillas Limestone of Moussa et al., 1987) appears to record the withdrawal of the sea at the end of the Miocene, followed by a rapid transgression in which the Camuy Fm was deposited. A final phase of uplift in the Pliocene hoisted much of this formation out of the sea.

Most authors have inferred from the absence of mid-Tertiary (and later) units in central Puerto Rico that an area roughly equivalent to the Cordillera Central Province has been continuously subaerial since the medial Oligocene (Lobeck, 1922; Hubbard, 1923; Sachs, 1959). However, for several reasons it is difficult to be precise about the subaerial area of ancestral Puerto Rico during the middle and latter part of the Cenozoic. The size of the island would have been significantly affected by bouts of uplift and subsidence during the Neogene as well as by globally synchronous eustatic fluctuations (Vail et al., 1977; Haq et al., 1987). Furthermore, at least 3500 m of subsidence has occurred along the trench-slope break in the Puerto Rico Trench since Miocene time (Perfit et al., 1980). Remarkably, undeformed limestones with ap-

parent dissolution features characteristic of karst (i.e., subaerial) environments have been identified at the 1200 m level in the Mona Canyon (Perfit et al., 1980). Given changes of this magnitude, coastline reconstruction is out of the question at present.

Monroe (1980: 57) stated that the absence of clastics in Aymamon rocks indicates that by the medial Miocene "the central part of Puerto Rico was a land of very low relief that probably stood not far above sea level." However, he concluded that there is no positive evidence that ancestral Puerto Rico was completely transgressed at any time during the Neogene. The only decisive evidence for transgression would have to be in the form of datable sedimentary units capping Older Complex rocks in the central interior. No such deposits have ever been identified in Puerto Rico (cf. Meyerhoff, 1933), which suggests that no mid-Tertiary transgression of this island was complete.

Williams (1969, 1989) has argued that Miocene transgressions may have seriously affected colonization opportunities in the Caribbean, especially for land mammals. Although there is as yet no direct evidence on the timing of the mammalian colonization of Puerto Rico, land reptiles lived there during the Early Miocene. This is of interest because this epoch is the one historically favored as the time of cataclysmic inundation in the West Indies (Schuchert, 1935: 17; Williams, 1969: 354).

COLLECTING FOSSIL VERTEBRATES IN PUERTO RICO

In addition to the evidence presented here, recent fossil discoveries in Hispaniola conclusively establish that terrestrial vertebrates colonized land masses in the Caribbean Sea at least as early as the middle Tertiary. The Hispaniolan evidence consists of well-preserved vertebrate specimens in amber, from localities in the northern part of the Dominican Republic. The age (or ages) of fossiliferous Dominican ambers is controversial, although most localities are probably of Early Miocene minimum age (Baroni-Urbani and Saunders, 1982; Brouwer and Brouwer, 1982). Specimens identified and described to date include an anole, *Anolis dominicanus* (Riepel,

1980); a gecko, *Sphaerodactylus dommeli* (Böhme, 1984); a frog, *Eleutherodactylus* sp. (of upper [?Late] Eocene age according to Poinar and Cannatella, 1987), and fragments of mammalian hair (Poinar, 1988). Although Dominican ambers will undoubtedly yield additional remains of very small (<5 g) terrestrial organisms, it is much less likely that animals in larger size ranges will be recovered therein. Thus the history of the majority of Caribbean land vertebrate lineages is going to have to be compiled from fossil discoveries made in more conventional paleontological contexts.

The purpose of the AMNH expeditions was to identify potentially fossiliferous contexts of various ages in various parts of Puerto Rico. We understood from the outset that this would be a daunting task, since none of the Greater Antilles possesses significant exposures of Tertiary sediments having a definitely terrestrial origin. With a handful of exceptions, the only contexts in which fossil vertebrates have been recovered in the West Indies are the usual microscale structures of karst terranes—caves, shafts, sinkholes, and mineral springs. Although such structures can be extremely rich in terms of fossil recovery (Olson, 1978; Pregill, 1981b), they have disadvantages. One is that they rarely preserve long paleontological records; the typical cave can act as a natural trap for terrestrial vertebrates only near the end of its ontogeny, when it possesses openings to the surface. Depending on the local rock fabric, weathering regime, and other factors, over time caves tend either to clog with sediments and breakdown or to erode to base level (cf. hominid bone caves of South Africa; Brain, 1975, 1981). Cave senility is likely to be accelerated in areas which have experienced tropical climatic conditions for geologically long periods. It is therefore unsurprising that, of the few directly dated cave faunas from the West Indies, none is demonstrably older than late Pleistocene (MacPhee et al., 1989; Morgan and Woods, 1986). Although it is possible that Tertiary fissure fills may exist in carbonate rocks on some islands, no fossiliferous ones have been identified with certainty.

In Puerto Rico at least, the best place to look for Tertiary land vertebrates may be the ample terrigenous deposits laid down by an-

cient rivers. The existence of Tertiary fluvial deposits on the island has been known for many years, but publication of detailed information on their location and origin is more recent (Monroe, 1966, 1976, 1980).

The first author to comment extensively on the hydrological history of Puerto Rico was Lobeck (1922). He believed that the large rivers ("ríos grandes") of the northern side of the island are extremely ancient features, and have always flowed essentially northward from the central highlands to enter the sea at approximately the position of their present mouths. This view went unchallenged until Monroe (1966, 1976) pointed to evidence for the comparative recency of this pattern of drainage. For example, the distal portion of the Río Grande de Arecibo, which now cuts through the center of the northern carbonate sequence, appears not to have existed before the end of the Miocene or beginning of the Pliocene, when large quantities of quartz sand derived from the Utuado batholith began to appear in Camuy rocks. Prior to that time, the section of the north coast between the present Río Guajataca and Río Grande de Manatí was a place of nearly pure limestone deposition. The Utuado batholith and nearby areas were instead drained by a river which entered the sea to the northwest, in the area between San Sebastián and Moca. It was not until uplift at the end of Aymamon time that interior streams were captured by the young Río Grande de Arecibo, then in the process of cutting through the northern coastal plain. Drainage reorganization of a similar sort led to the creation of the modern Río Grande de Manatí, which has captured the headwaters of rivers that previously drained to the northwest and northeast. According to Monroe (1980: 42), rivers were prevented from draining to the north in pre-Camuy time by the topography of ancestral Puerto Rico. Downwarping of both the north and south coasts during the Late Miocene no doubt facilitated the change in drainage direction of interior streams.

Two of Monroe's hypothesized Tertiary river drainage basins are of particular importance here because fossil vertebrates have been recovered from sediments deposited by them. Since the precise courses of the rivers that drained these basins are not known, we

simply identify them as the western and eastern paleodrainage complexes.

WESTERN PALEODRAINAGE COMPLEX: Monroe (1980) argued that the presence of "cobble sand" in San Sebastián and Lares sediments outcropping between the towns of San Sebastián and Moca indicates that a very large river reached the sea in this area at least as early as the medial Oligocene. No identifiable trace of the valley for this river exists on the modern surface, although the preferred direction of drainage in this part of the island seems to have trended toward the northwest until the Middle Miocene (Monroe, 1980).

Sedimentological evidence for Monroe's great western river is poor during late Middle and Late Miocene time, apparently because erosion had considerably lowered the land surface by this time. However, indicative of this river's continued, if diminished, existence is the fact that Aguada and Aymamon limestones in this part of Puerto Rico contain more clastics than do outcrops slightly further east (Monroe, 1980). At the end of the Aymamon deposition, the center of the island was upbowed along an east-west axis, rejuvenating the old rivers draining the highlands. As noted previously, during this period drainage patterns were reorganized. Some of the modern rivers flowing northward in this part of the island (Camuy, Tanamá, Arecibo) probably now drain areas originally within the catchment of the great northwestern river.

EASTERN PALEODRAINAGE COMPLEX: From San Sebastián through Cibao time, part of the eastern complex seems to have drained to a river whose mouth was near Corozal. This is suggested on the one hand by the considerable quantities of gravel encountered in San Sebastián facies in the Corozal area, and on the other by the fluvial/estuarine character of the Miranda Sand outcropping slightly to the north of this town. The position and sediment load of this river varied, because the Miranda Sand exposure north of Corozal is underlain by the relatively pure limestone of the Quebrada Arenas Lm. The Miranda Sand contains jasper derived from the Barranquitas area in central Puerto Rico (Monroe, 1980). At present, this area is drained by the headwaters of several rivers, including the

Río Grande de Manatí and Río Cibuco. Several other penecontemporaneous rivers drained out of the highlands into the area between Corozal and Bayamon, where they deposited the Mucarabones Sand. Among these were the ancestral Río de la Plata, Río Bayamon, and Río Piedras, all of which "had courses in the uplands different from the courses they have today, and all were actively eroding during Lares and Cibao time" (Monroe, 1980: 27–28).

As in the far west, the Aguada and Ayamamon were periods of diminished terrigenous deposition. Monroe (1980) believed that the river which deposited the Miranda Sand was, however, still somewhat active during deposition of the Aguada Limestone because quartz grains occur in lenses in rocks of that age north of Corozal but not elsewhere in the vicinity.

The paleohydrology of southern Puerto Rico has not been worked out in comparable detail. However, river activity was apparently present early in the Oligocene, for Monroe (1980) has identified loose sands of the uppermost Juana Diaz Fm (?Middle Miocene) as a possible channel fill at one site near Ponce. These deposits have so far yielded only a few scraps of chelonian shell (see Catalog), but this is a hopeful sign in view of the wealth of fossil material now known from similar contexts in northern Puerto Rico.

THE RABELL COLLECTION

Some of the fossils described in this report come from an extensive collection amassed in the first quarter of this century by a resident of San Sebastián, Narciso Rabell Cabrero. The vertebrate material in the Rabell collection was donated to the American Museum of Natural History in 1987 by its custodians, Dr. Gualberto Rabell of San Juan and Mrs. Narcisa Rabell de Olivera of San Sebastián. The balance of the collection, consisting of several thousand specimens of marine invertebrates, was given to the museum of the Departamento de Biología, Universidad de Puerto Rico, Río Piedras. We take this opportunity to acknowledge our thanks to the Rabell family on behalf of the AMNH and to provide a few remarks on Narciso Rabell and his collection.

From an early age, Narciso Rabell was an avid natural historian and amateur invertebrate paleontologist. Over the years he built up a remarkably diverse collection of invertebrates from Oligo-Miocene formations in the vicinity of San Sebastián, all originally labeled as to species and locality. This collection was profitably studied by various members of the Scientific Survey of Puerto Rico and the Virgin Islands, organized in 1913 by the New York Academy of Sciences (Britton, 1919). Rabell's courtesy and help to these scientists is commemorated in their acknowledgments and, as permanent tribute, in the names they gave to various new species from localities first prospected by him (e.g., *Clementia rabelli*, Maury, 1920; *Atrina rabelli*, Hubbard, 1920). From correspondence preserved by the Rabell family, it is clear that he was held in high esteem by leading invertebrate paleontologists in Europe and the United States, with whom he freely traded specimens and data until his untimely death in 1927.

Although Rabell's interests were mainly conchological, as opportunity offered he collected vertebrate fossils as well. Given his great industry, it is not surprising that he eventually gathered excellent material of sirenians, chelonians, crocodilians, selachians, and teleosts—in short, all of the major marine vertebrate groups now known from Puerto Rico. The earliest document relating to these fossils is Rabell's (MS) catalog of material placed on public display at "La Tercera Feria Insular" in San Juan in 1913. In this catalog he specifically identified one jaw in his possession as being "like that of the manatí," but various large mammalian postcranials, undoubtedly sirenian, were described as "more like those of the rhinoceros and especially the tapir than of any other animals" (trans.). Photographs of an axis and a scapula from this exhibit were published, with a text, in the following year (Rabell, 1914). A later paper (Rabell, 1924) dealt with his extensive collection of selachian teeth. He was obviously planning to publish additional papers on Puerto Rican fossil vertebrates, because in 1924 he brought much of his collection to New York in order to undertake comparisons with material at the AMNH and Columbia University. Declining health after

his return to Puerto Rico must have prevented the realization of his plans.

Some years after Rabell's death, his family carefully packaged his specimens and placed them in storage. Unfortunately, they had no means for protecting the papers and manuscript catalog stored with the fossils, and these were ultimately destroyed by insects. As a result, all of the information needed to connect specific fossils to specific localities has now been lost, save for those few instances in which other researchers described specimens (exclusively invertebrates and plants) found at sites shown to them by Rabell. Although the Rabell fossils remain highly significant, the loss of provenance data naturally affects their scientific value. In 1987 we attempted, through interviews with Rabell family members and associates, to ascertain the likeliest collecting areas for the fossil sirenians and turtles. Messrs. Tomás Magin and Augustin Vélez of San Sebastián collected, as boys, with Rabell in the 1920s. They recall having found turtle shells and large ribs along the Quebrada Collazo, a creek between San Sebastián and Lares which is lined with deposits of San Sebastian age. This creek is perhaps the most famous paleontological locality in Puerto Rico (see Catalog), and has been repeatedly visited by paleontologists and paleobotanists since Rabell first made its existence known to the Scientific Survey. Unfortunately, as far as we have been able to determine, no vertebrate remains were ever recovered from the gorge of the Collazo by the members of the Survey or any later workers; we were similarly unsuccessful in our explorations during 1987 and 1988.

FOSSIL VERTEBRATES FROM OLIGOCENE AND MIOCENE LOCALITIES OF PUERTO RICO

EARLY MIOCENE SQAMATES

Potentially the most important finds made during the 1988 season were two small, badly damaged squamatan vertebrae recovered from a lignitic, clayey sand that overlies poorly sorted pebbly conglomerate at AMNH loc. PR 88-1 (fig. 4E). Because the majority of fossils recovered at this site were extremely friable, whenever possible we carved them out in blocks so that they would be supported

by matrix upon removal from the ground. The matrix/fossil blocks were then wrapped in tissue and immediately stowed in plastic boxes or bags. We did not discover that we had definite evidence for the presence of both Ophidia and Sauria in the Puerto Rican Miocene until we began to prepare our material in the laboratory. Although it is regrettable that better fossils were not collected, these finds are significant enough to deserve preliminary notice here. Formal description of these remains will be undertaken by Max K. Hecht (CUNY), to whom we are indebted for helpful systematic and morphological discussions.

Boid

AMNH-VP 24562 (fig. 5, table 1) can be diagnosed as an ophidian vertebra because its zygosphenes-zygantrum complex is one typical for snakes (i.e., wide zygosphenic tendon with overhanging, acute articulations, nonarticular area between zygosphenic and zygapophyseal facets, anterodorsal lip without deep notch; Hoffstetter and Gasc, 1969). Although the overall condition of the fossil is poor, most structures are preserved on one side or the other. This permitted the reconstructions illustrated in Figure 5, although the outline of some features is conjectural.

Among ophidians, the specimen most closely resembles vertebrae of Boidae, especially in exhibiting the following features: (1) centrum is stumpy, being broader (between rib articulations) than long; (2) subcentral ridges on centrum are prominent; (3) zygosphenes is massive relative to rest of specimen; (4) prezygapophyseal processes are blunted, not elongated; (5) neural arch is markedly vaulted; (6) interzygapophyseal ridge is prominent; and (7) low but distinct keel (hypapophysis) is present on ventral surface of centrum. Taken together, traits (1) – (6) suggest that this specimen is more likely to belong to a boid than to any other ophidian. If it does represent a boid, trait (7) indicates that AMNH-VP 24562 is most probably an anterior dorsal vertebra.

The only extant boid on Puerto Rico or its offshore islands is *Epicrates*, whose center of species diversity is the Greater Antilles (Schwartz, 1978; Kluge, 1988). AMNH-VP

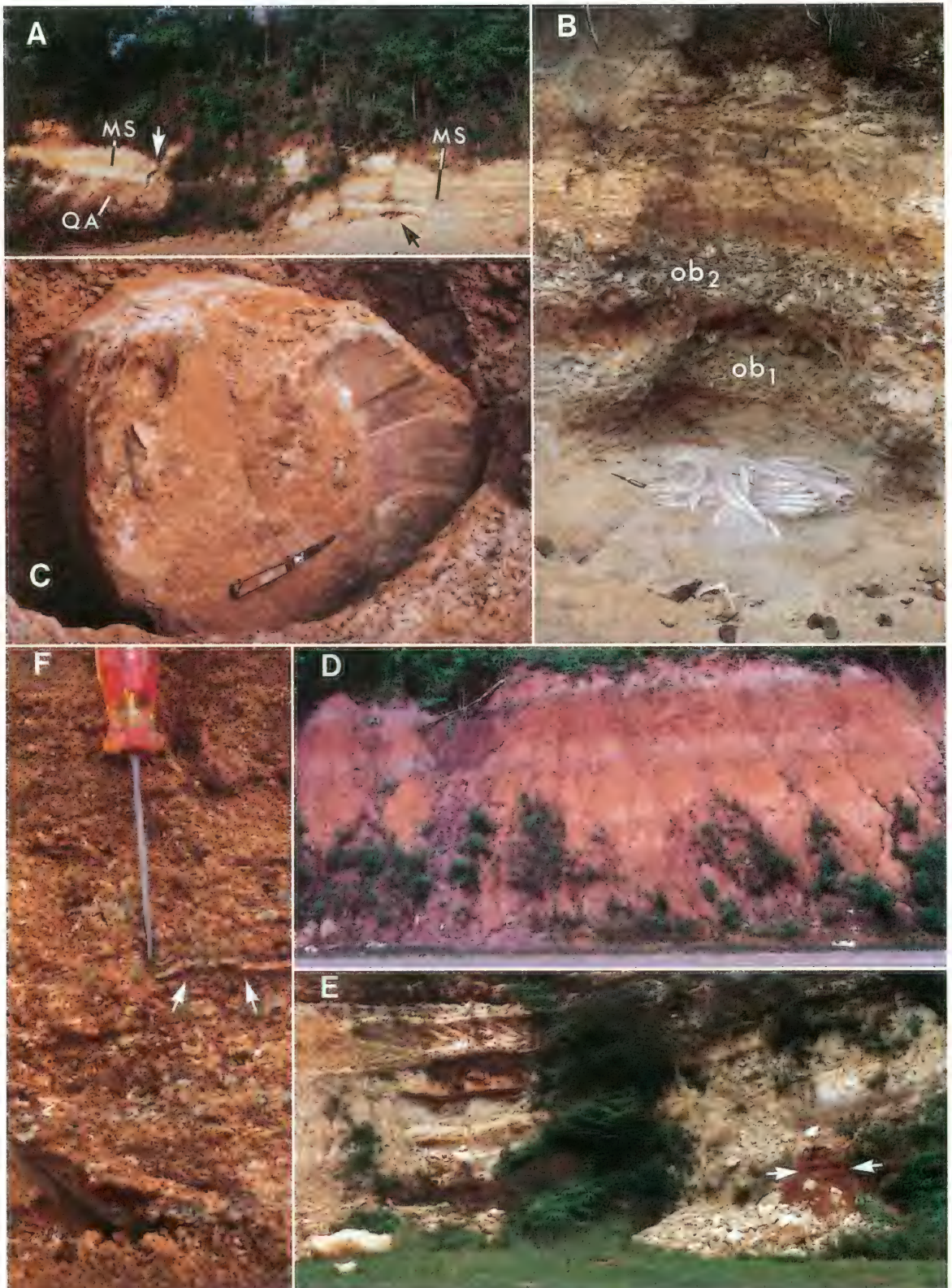


Fig. 4. A, View of exposure of Early Miocene Miranda Sand (Cibao Fm) at AMNH loc. PR 87-4, looking north from Highway 820. The unconformity between Quebrada Arenas Lm (QA) and Miranda

TABLE 1
Representative Measurements (in mm) of Reptilian Vertebrae from AMNH Locality PR 88-1^a

Taxon/AMNH no.	Vertebra	Measurement	Value (in mm)
Boidae, <i>gen. sp. indet.</i> AMNH-VP 24562	anterior dorsal?	width, maximum transverse, bi-prezygapophyseal	14.5
		width, maximum transverse, bi-postzygapophyseal	13.8
		width, maximum transverse, of cotyle	5.4
		height, dorsoventral, of neural canal	2.5
		height, dorsoventral, dorsal rim of zygantrum to ventral rim of cotyle	9.5
		length, anteroposterior, ventral rim of cotyle to posteriormost point on condyle	6.7
		length, maximum anteroposterior, between pre- and postzygapophyses	11.5
		length, anteroposterior, of neural arch, rostral margin of zygantrum to base of neural spine	8.7
?Iguanidae, <i>gen. sp. indet.</i> AMNH-VP 24500	dorsal or posterior cervical?	width, maximum transverse, bi-prezygapophyseal	—
		width, maximum transverse, bi-postzygapophyseal	—
		width, maximum transverse, of cotyle	8.5
		height, dorsoventral, of neural canal	3.2
		height, dorsoventral, dorsal rim of zygantrum to ventral rim of cotyle	—
		length, anteroposterior, ventral rim of cotyle to posteriormost point on condyle	15.0*
		length, maximum anteroposterior, between pre- and postzygapophyses	18.1
		length, anteroposterior, of neural arch, rostral margin of zygantrum to base of neural spine	13.1

^a Measurements not reflecting true values because of breakage of bone are followed by asterisks.

24562 differs from anterior dorsals of *E. inornatus* of mainland Puerto Rico in several respects, including general robusticity, centrum proportions, orientation and size of the zygapophyseal facets, degree of elaboration of the interzygapophyseal ridges, heaviness of laminae, and height vs. length of vertebra as seen in lateral aspect (fig. 5A–O). AMNH-VP 24562 resembles dorsal vertebrae of the Miocene Floridian boid *Pseudoepicrates stanolseni* (Auffenberg, 1963) in such features

as the definition of the interzygapophyseal ridges and laminar heaviness, but the resemblances are not so strong as to suggest identity. No specimens of the endangered (and perhaps now extinct) Mona Island boid, *E. monensis*, were available for comparison. *Epicrates inornatus* and *monensis* differ in the number of dorsal markings and subcaudal scales, but are otherwise said to be very similar (Rivero, 1978). Kluge's (1988) analysis of lipid, external morphological, and osteo-

←
Sand (MS) can be seen at the left. Arrows indicate locations where sirenian jaw (white arrow) and axial skeleton (black arrow) were recovered. **B**, Close-up of sirenian axial skeleton from AMNH loc. PR 87-4 in process of being excavated; note position of large oyster beds (ob1, ob2). **C**, Large pleurodiran turtle, also from AMNH loc. PR 87-4, in process of being excavated. **D**, View of typical mottled clays of Late Oligocene San Sebastian Fm, exposed along Highway 111 near San Sebastián. **E**, View of lower portion of cliff face at AMNH loc. PR 88-1, as seen from Highway 2. Arrows enclose position in brown sand where boid and ?iguanid vertebrae were discovered. Sand is referred to Early Miocene Cibao Fm (undifferentiated, but probably either Guajataca or Upper Mbr); light-colored limestone above sand represents Middle Miocene Aguada Fm. **F**, Close-up of fossiliferous brown Cibao sand at AMNH PR loc. 88-1, to illustrate texture. Note microstratification and presence of fine gravel. Arrows point to small piece of turtle shell.

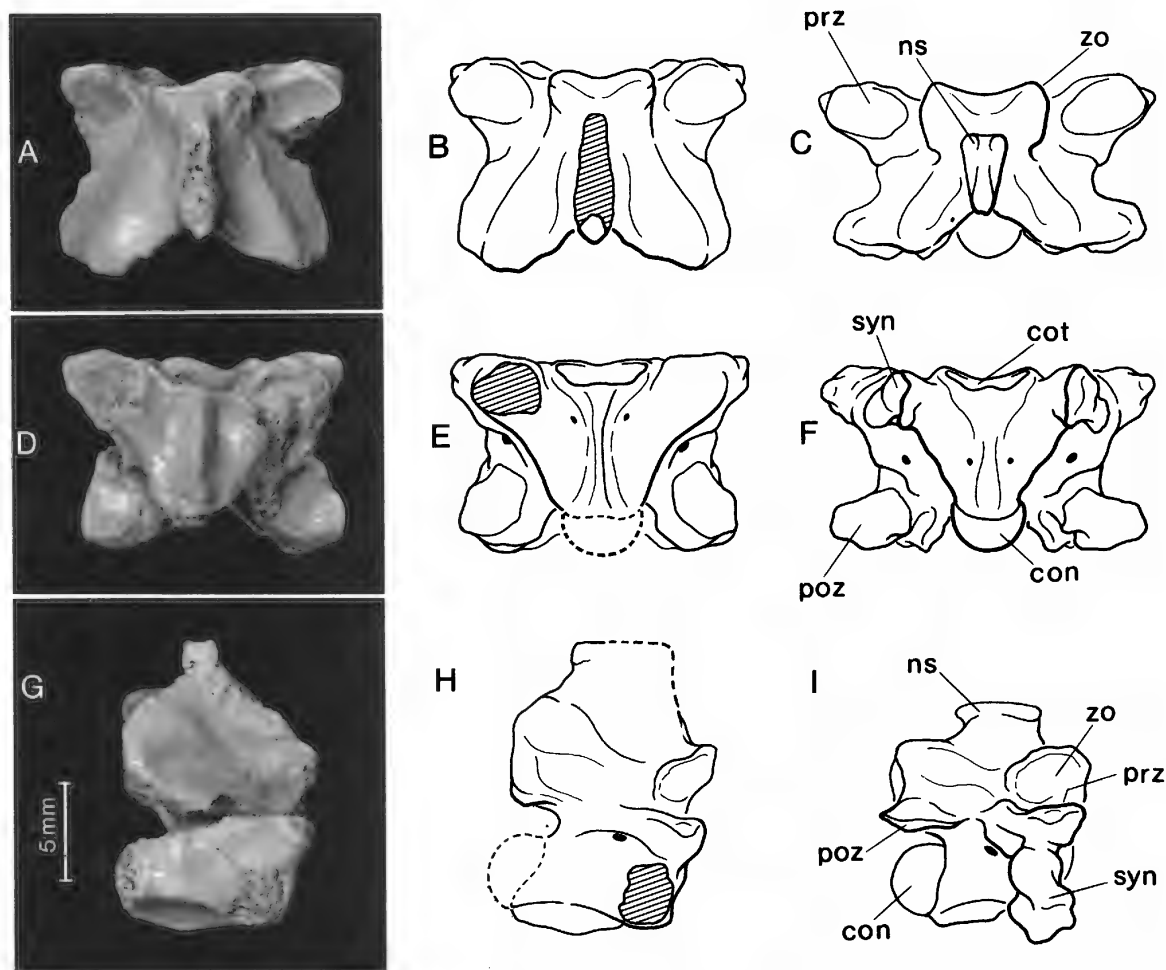


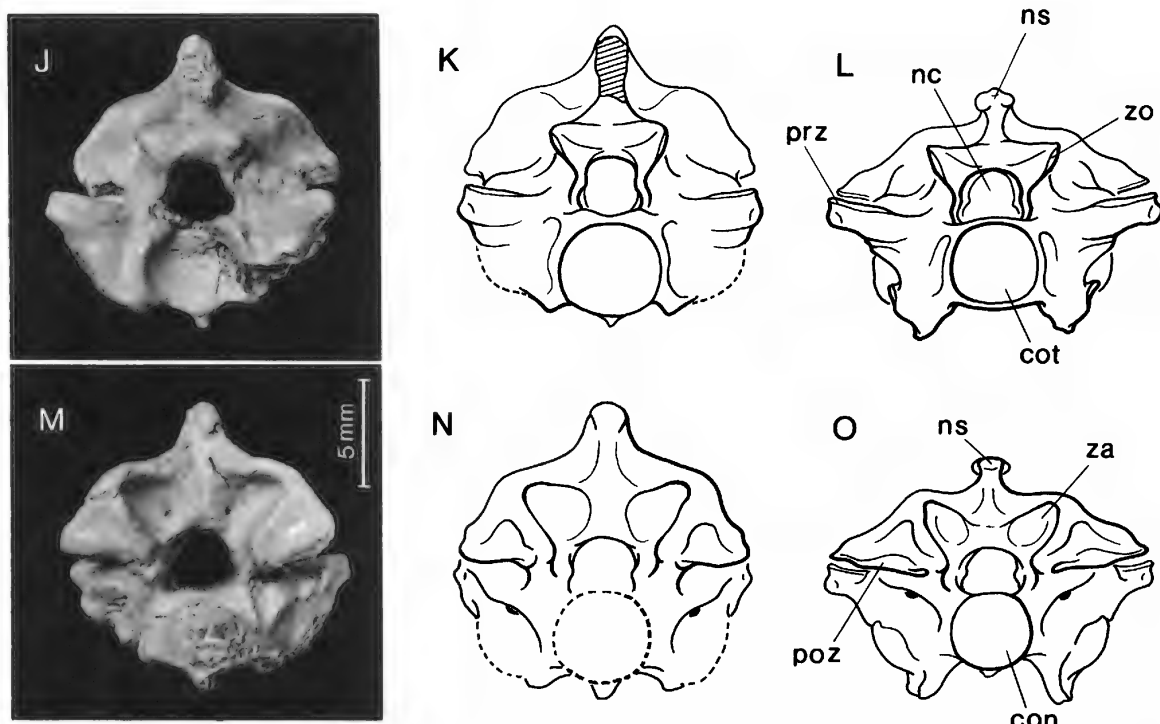
Fig. 5. Incomplete ?anterior dorsal vertebra of a large boid (AMNH-VP 24562) from AMNH loc. PR 88-1 (photos, A, D, G, J, M; reconstructions, B, E, H, K, N), compared to an anterior dorsal of

logical character sets for *Epicrates*, however, indicates that *monensis* has shared a more recent common ancestry with Hispaniolan *fordii* and *gracilis* than with Puerto Rican *inornatus*. The other extant boids of the West Indies—*Corallus*, *Boa*, and *Tropidophis*—do not occur in Puerto Rico. None displays strong resemblances to the fossil, and we provisionally conclude that it is improbable that the species represented by AMNH-VP 24562 is congeneric with any of them.

At this stage there is no justification for concluding anything other than that AMNH-VP 24562 represents a boid snake, possibly but not certainly a boine. It is evidently not the same as Puerto Rican *Epicrates*, but where it belongs in relation to known taxa will require detailed study.

?Iguanid

AMNH-VP 24500 (fig. 6, table 1) is in very poor condition, and our allocation of this specimen to Iguanidae is provisional. The specimen appears to be a dorsal or possibly a posterior cervical, and is very large. The gracility of the deeply notched zygosphenon, slender profile of the centrum (in lateral view), elongated vertebral notch, position of the condyle on a long neck, and outward angulation of the postzygapophyseal facets are saurian rather than ophidian features. It must therefore represent a species different from AMNH-VP 24562. The zygosphenon and zyganchtrum are well developed, a feature that (among lizard families) is seen only in large species of Varanidae, Teiidae, and Iguanidae.



extant *Epicrates inornatus* (AMNH-HI 70023) from Puerto Rico (C, F, I, L, O). Views are: dorsal (A, B, C in first row), ventral (D, E, F in second row), lateral (G, H, I in third row), anterior (J, K, L in fourth row), and posterior (M, N, O in fifth row). Reconstructions of fossil are presented to facilitate comparisons with living boid. Borders that are bilaterally damaged on fossil are of uncertain shape, and are depicted by broken lines in the reconstructions. Other defects are indicated by hatchure.

Gekkonidae, Scincidae, and Anguinidae—all of which have Recent Puerto Rican representatives—can therefore be excluded from consideration.

Because of the condition of the specimen, it is difficult to choose among these three potential alternatives, and our comparisons have not been exhaustive. Although monitors do not exist in the New World at present, sanidine varanids were present in North America until the end of the Paleogene (Romer, 1956; Estes, 1983) and therefore cannot be excluded from consideration on biogeographical grounds. However, the upwardly facing condyle, characteristic of varanids (Romer, 1956), is apparently absent in the fossil. The New World teiids have an existing distribution that extends into the insular Neotropics. However, none of the truly large teiids is an island-dweller. Dorsal vertebrae of the large South American teiid *Tupinambis* are similar to the fossil, although the former have a comparatively smaller cotyle and a stouter centrum. The cotyle is larger and the centrum is

comparatively longer in iguanid dorsal vertebrae, which appear to represent the best overall match for the fossil. AMNH-VP 24500 differs markedly from the rock iguanid of Puerto Rico (*Cyclura cornuta*) in having an exceptionally wide vertebral notch, as well as in details of proportion. Only the root of the neural spine is preserved; the spine seems to have been comparatively gracile and restricted to the caudal half of the neural arch. This is somewhat surprising in view of the generally large size and robusticity of the neural spine in iguanid dorsals. However, there are exceptions within the family: the iguanines *Sauromalus* and *Ctenosaura* exhibit comparatively short spines, and some other species display important ontogenetic variation in the degree of spine development (De Queiroz, 1987).

Discussion

The snake and lizard vertebrae from AMNH loc. PR 88-1 are the first direct evi-

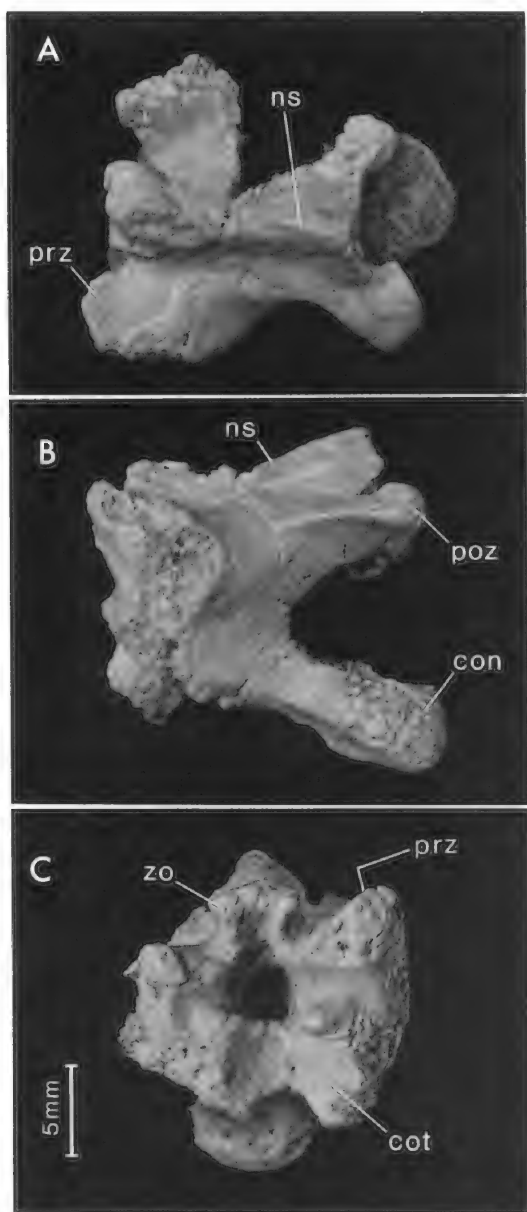


Fig. 6. Partial dorsal or cervical vertebra of a large lizard (AMNH-VP 24500), provisionally identified as iguanid, from AMNH loc. PR 88-1. Views are: A, posterior (anterior end to right); B, lateral (anterior end to right); and C, anterior.

dence that reptiles other than turtles and crocodiles existed in Puerto Rico as long ago as the Early Miocene. Family diagnosis for the ?iguanid is provisional, and better evidence may show that it is in error. Caution in formulating conclusions is therefore appropriate:

(1) AMNH-VP 24500 and 24562 do not represent species that are part of the known extant or recently extinct herpetofauna of Puerto Rico (Pregill, 1981b), although they appear to belong to families with wide representation in the West Indies.

(2) Almost all lizards and snakes are adapted to terrestrial habitats; among the "marine" squamates, only a few elapids and hydrophiids can be described as exclusively aquatic, and none of these is known to have lived in the Caribbean. The semiaquatic adaptation of the Galapagos iguanid *Amblyrhynchus* is unique within its family (which includes several other insular—but wholly terrestrial—taxa). The presence of a boid and an ?iguanid in Puerto Rico during the Early Miocene is reasonably interpreted as evidence that some portion of this island was then emergent.

(3) All extant snakes are carnivorous, so it is reasonable to assume that the boid from AMNH loc. PR 88-1 was as well. Living boids (especially boines) are predominantly predatory upon birds and mammals, although they will eat other vertebrates (including other snakes, lizards, and frogs; Rivero, 1978). Boids resident on islands are probably fairly catholic feeders, and therefore we cannot conclude that the presence of a boid during the Early Miocene of Puerto Rico is inferential evidence for the presence of warm-blooded vertebrates. We take our discovery as a hint, and nothing more, that Puerto Rico could have supported a variety of terrestrial vertebrates at that time.

As already noted, the recovery of one or two extinct taxa from Tertiary contexts in Puerto Rico is of little importance as a critical test of mechanisms of faunal formation in the West Indies. From a dispersionist viewpoint, the fact that the only terrestrial vertebrates recovered at AMNH loc. PR 88-1 were a boid and an ?iguanid is exceptional, because members of these families have, on several occasions, managed to occupy (or reoccupy) islands that were "sterilized" by cataclysmic events. In these cases, over-water rafting is the only reasonable explanation for their presence (e.g., repopulation of Krakatau by *Python reticulatus* and other reptiles subsequent to the eruption of 1888 [Dammerman, 1948; Thornton and Rosengren, 1988];

colonization of Aldabra atoll by the Malagasy iguanid *Oplurus* on at least two occasions during the late Pleistocene [Taylor et al., 1979]).

The squamatan fossils from AMNH loc. PR 88-1 are nevertheless important in other respects. We now know, for certain, that conditions favorable for the colonization of Puerto Rico by land vertebrates must have existed at least as early as the Early Miocene. We also now know, for certain, that there have been extinctions in Puerto Rico other than those which occurred in the late Pleistocene or Holocene, because squamatans like those from AMNH loc. PR 88-1 are not represented in the Quaternary record. While we still know almost nothing about the diversity of Puerto Rico's fauna during the mid-Tertiary, a start has been made. What is needed is a willingness on the part of researchers in a variety of paleobiological disciplines to devote some substantial portion of their time to resolving how this fauna was formed. Recovery of a few marsupials, carnivorans, or ungulates—merely to mention those mammalian groups that always end up being mentioned in discussions of West Indian biogeography—from Paleogene or early Neogene contexts in the Antilles would probably not be decisive in everybody's eyes. But it would not be irrelevant, because one's acceptance of either dispersion or vicariance as the dominant mode of faunal formation in the West Indies will probably continue to be based on one's assessment of the probabilities. For our part, we remain agnostic about the claims of both camps, and encourage others to contribute to what is easily one of the most intriguing problems in historical biogeography.

OLIGOCENE AND MIOCENE SIRENIANS

The first Puerto Rican sirenian fossils to be described in the scientific literature were collected along the Río Jacaguas (fig. 2) in 1915 by Reeds (1916); Matthew (1916) identified these fossils as dugongid and referred them to *?Halitherium antillense*. A half-century later, Reinhart (1959) recognized and named a second sirenian, *Caribosiren turneri*, on the basis of material from the San Sebastián-Lares area (some of which had been collected by Narciso Rabell). Although addi-

tional sirenian fossils have been recovered since then, none has been described in detail.

Metaxytherium, cf. *M. calvertense*

Metaxytherium or its close relatives have been found in Pliocene and Miocene marine deposits on both sides of the Atlantic (Kellogg, 1966; Reinhart, 1976; Domning and Thomas, 1987) as well as the Pacific side of northern South America (Muizon and Domning, 1985), and its presence in the eastern central Caribbean is therefore unremarkable. Our provisional identification of *Metaxytherium*, cf. *M. calvertense*, in Early Miocene Miranda Sand deposits in northern Puerto Rico is based on features of an incomplete jaw (AMNH-VP 125780) found at AMNH loc. PR 87-4 (see Catalog; figs. 4A, 7). We refer to the same taxon a partial axial skeleton (AMNH-VP 125781) found at the same locality, about 20 m west of the place where the jaw was recovered and at a slightly lower stratigraphic level (fig. 4A, B). Pertinent measurements of these specimens are presented in tables 1 and 2.

REFERRED MATERIAL: The left side of the referred jaw (AMNH-VP 125780) bears four worn and fractured cheekteeth (m1-3 and dp5, in the conventional enumeration of tooth loci). The right side consists only of the anterior end of the corpus; it retains one tooth, the m2. The corpora and teeth have been crushed into each other by sediment pressure and proved impossible to separate during preparation.

The jaw is typically dugongid in form (fig. 7). The anterior ends of the corpora are strongly deflected downward; they appear to have been ankylosed at the symphysis, although this point was difficult to check because of compression. The length of the left side of the jaw, from condyle to anterior end, is 290 mm and its minimum depth under the tooth row is 63 mm. A broad gutter for the mandibular nerve becomes an enclosed canal beneath the anterior margin of dp5. Beneath m2 and m3, a large foramen of uncertain function opens into the gutter for the mandibular nerve. The coronoid process is triangular and does not seem to have been strongly hooked. The condyle is nearly square in outline and approximately level with the

coronoid. The ascending ramus is anteriorly inclined and in dorsal aspect overhangs the posterior loph of the last molar. The angle and ventral margin of the corpus are not preserved.

Crushing also makes it difficult to ascertain the number of alveoli anterior to the preserved teeth. Even so, it can be reasonably inferred from the left mandibular corpus that there were probably only four lower teeth on each side, since on this side there are no al-

veoli in the 50 mm of well-preserved bone in advance of the premolar (fig. 7).

The dp5 bears two roots, the anterior of which was broadly exposed during life as a result of wear. Although the crown's occlusal surface is worn through, it is clear that the tooth was bilobate, with the posterior loph being larger in width than the anterior.

The molars are also heavily worn. Like dp5, m1 is also bilobate, but with the opposite proportions (anterior loph larger than posterior loph). No crown features are preserved, the occlusal surface merely consisting of a dentine lake surrounded by enamel borders. Much the same combination of features is seen in the badly damaged right and left m2s. The exposed posterior root of the right m2

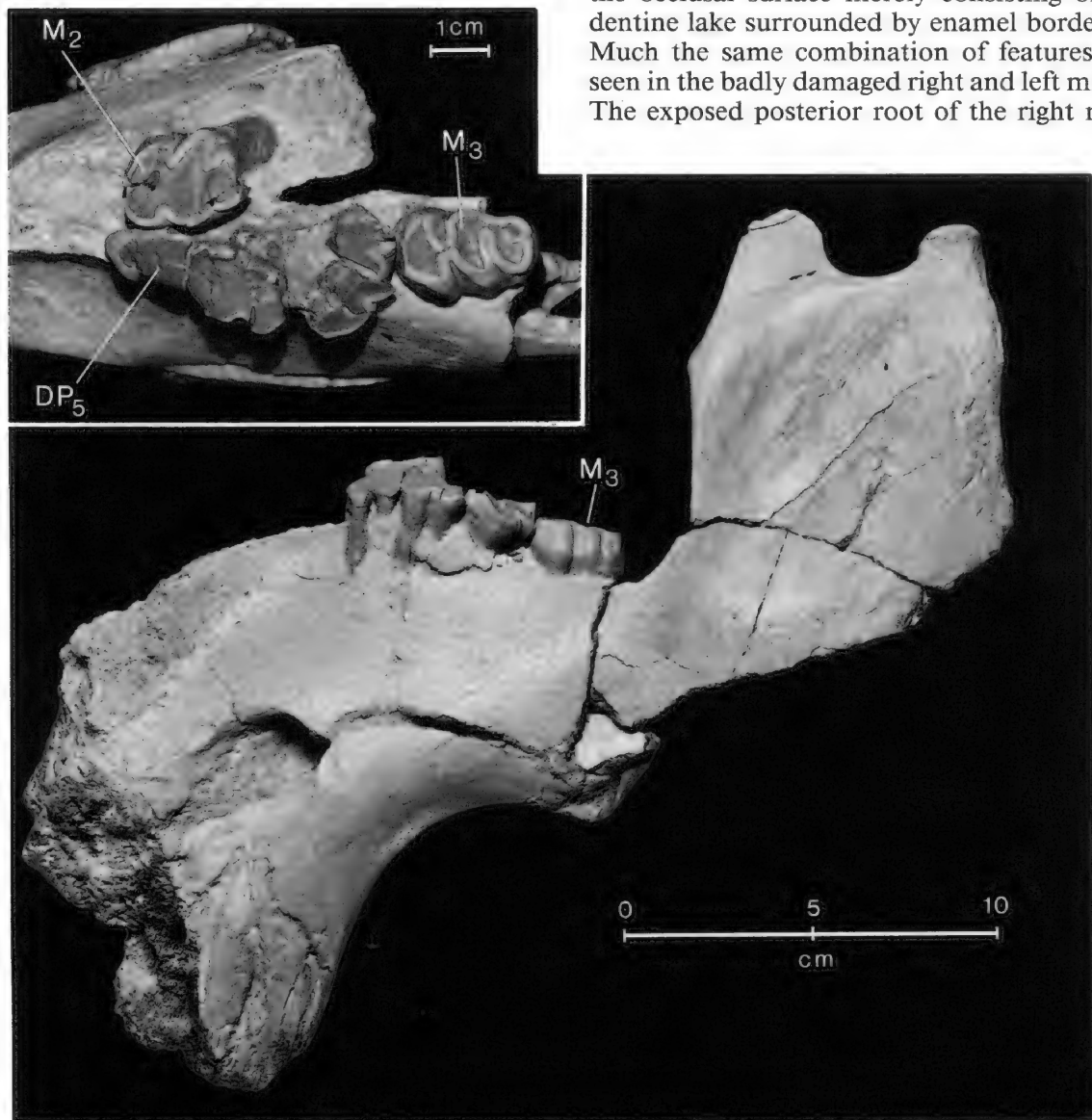


Fig. 7. Lateral view of mandible (AMNH-VP 125780) recovered at AMNH loc. PR 87-4 and referred to *Metaxytherium*, cf. *M. calvertense*. Inset, occlusal view.

TABLE 2
Representative Measurements (in mm) of Miranda Sirenians from AMNH Locality PR 87-4^a

Taxon/AMNH No.	Element	Measurement	Value (in mm)
<i>Metaxytherium</i> , cf. <i>M. calvertense</i> AMNH-VP 125780	left mandible	length, condyle to anterior end of jaw	290*
		height, minimum, of mandibular corpus	62
<i>Metaxytherium</i> , cf. <i>M. calvertense</i> AMNH-VP 125781	atlas	width, maximum mediolateral	140
	atlas	height, maximum dorsoventral	85
	atlas	height, internal	53
	axis	height, maximum dorsoventral	95*
	axis	height, dorsoventral, of cotyle	30
	third cervical	thickness, anteroposterior, of centrum	14
	third cervical	width, maximum mediolateral	100
	third cervical	height, maximum dorsoventral	79
	third cervical	width, mediolateral, of vertebral canal	44
	third cervical	height, dorsoventral, of vertebral canal	28
	fourth cervical	width, maximum mediolateral	124
	fourth cervical	height, maximum dorsoventral	90*
	fifth cervical	width, maximum mediolateral	140*
	first thoracic	width, maximum mediolateral	165
	first thoracic	height, maximum dorsoventral	90
	third thoracic	width, maximum mediolateral	160
	third thoracic	height, maximum dorsoventral	155
	third thoracic	width, anterior articular surface of centrum	50
	third thoracic	height, anterior articular surface of centrum	29
	seventh thoracic	height, dorsoventral, from tip of spinous process to posterior face of centrum	147
Sirenian, <i>gen. sp. indet.</i> AMNH-VP 125782	?second thoracic	width, mediolateral, of vertebral canal	17
		height, dorsoventral, of vertebral canal	17
		width, maximum mediolateral	72*
		width, mediolateral, of centrum	28*

^a Measurements not reflecting true values because of loss or breakage of bone are followed by asterisks.

is anteroposteriorly compressed and 25 mm in length.

The m3 is distinctive in being elongate and trilobate ("obovate" in outline; Reinhart, 1976). Although it is less worn than the more anterior cheekteeth, features of the occlusal surface have mostly been lost. The anterior cusps have been reduced through wear to a single anterior loph which is isolated from the posterior talonid by vestiges of a transverse valley. This loph does not bear an anterior cingulum. A medial loph is defined posteriorly by a transversely directed finger of enamel. The dentine lake of the medial loph is narrowly confluent distolingually with that of the posterior (hypoconulid) loph. Apart from a hooklike projection of enamel at the posterolingual corner, no evidence of posterior cusps or cuspules persists. The distal two-

thirds of the anterior root of m3 is exposed through the lingual mandibular surface. This root appears to be compressed anteroposteriorly and is approximately 35 mm in length. The posterior root, visible through a break in its alveolus, is completely housed in bone and its apex is well separated from the mandibular canal.

The axial skeleton from the Miranda Sand (consisting of C1-7, T1-16, and numerous costal elements) is in better condition (fig. 4B). There are definitely seven cervical vertebrae, as in dugongids but not *Trichechus* (which possesses only six). The atlas (fig. 8) was found about 2 m away from a mass that included the other cervicals and first two thoracics, but at the same stratigraphic level. The vertebral canal of the atlas is hourglass shaped, due to the form and projection of the odon-

TABLE 3
Mandibular Tooth Dimensions of AMNH 125780
and Other Sirenian Specimens Assigned to *Me-
taxytherium calvertense* (in mm)

Tooth	Dimen- sion ^b	Sources ^a			
		Puerto Rico	Peru	Mary- land	Cuba ^c
Ldp5	ML	17.0	—	—	—
	AW	11.0	—	—	—
	PW	13.0	—	—	—
Lm1	ML	19.0	17.3	—	15.0
	AW	15.0	14.4	—	12.2
	PW	—	15.5	—	12.2
Rm2	ML	22.0	23.3*	21.0	16.8
	AW	16.0	15.7	15.0	13.4
	PW	17.0	17.5	—	14.4
Lm3	ML	25.0	28.0*	—	21.2
	AW	17.0	22.0*	—	15.6
	PW	12.0	21.5*	—	16.2

^a Sources of material: Puerto Rico (this report [AMNH-VP 125780]); Peru (after Muizon and Domning, 1985 [Muséum National d'Histoire Naturelle-Institut de Paléontologie PRU 7]); Maryland (after Kellogg, 1966 [USNM-NH 23271]); and Cuba (after Varona, 1972 [Museo Felipe Poey 1255, holotype of *M. riveroi*]).

^b Dimensions: ML, mesiodistal length; AW, buccolingual width of anterior loph; PW, buccolingual width of posterior loph. Measurements are of single teeth (L, left; R, right) except in case of m2 and m3 of Cuban material, which are averages of right and left teeth of holotype jaw of *M. riveroi*. Values followed by asterisks are estimates.

^c Daryl P. Domning (personal commun.) believes that the teeth represented in the mandibular dentition of the holotype of *M. riveroi* are dp5–m2, not m1–m3 (contra Varona, 1972). If this is correct, the dental dimensions of the Cuban fossil are not markedly smaller than (other) *calvertense*.

toid and the neural arch. This is a resemblance to dugongids; *Trichechus* has a less indented vertebral canal (Reinhart, 1976). The transverse processes of the atlas are relatively slender and subhorizontal. The right transverse process is pierced by a vestigial foramen transversarium; on the left side the course of the vertebral artery is marked by a notch. There are also notches or partial foramina for the first cervical nerve on the neural arch.

Only part of the right half of the axis is preserved (fig. 8). It was not ankylosed with C3 (cf. description of vertebral elements from

Rabell collection). A distinctive feature of the axis is the massive and irregularly shaped spinous process on the dorsal aspect of the neural arch. The remaining cervicals are mostly incomplete. The broad, winglike transverse processes increase greatly in size, at least between C3 and C5. Centra are preserved only for C3–5, but they appear to have progressively increased in depth. The seventh cervical bears a short spinous process.

The 3rd through 16th thoracic vertebrae were found in direct articulation a short distance away from the group composed of the cervicals and first two thoracics. Although this part of the spinal column is slightly crushed, its preservation is generally excellent. As most of these vertebrae have not been disarticulated or fully prepared, we offer only a cursory description. There is excellent morphological correspondence to the thoracics of *Metaxytherium calvertense*, described in great detail by Kellogg (1966). The centra of T2 through T9 bear anterior and posterior demifacets (not visible on T1); thereafter only the anterior facet is present. The longest transverse processes occur on T1; posteriorly, these processes become progressively less prominent. The anterior borders of the spinous processes are relatively straight, while on the posterior margin there is a broad indentation basally. Numerous ribs and rib fragments, not described here, were found in close proximity to the thoracics.

COMPARISONS AND DISCUSSION: Features of the jaw ally this Miranda sirenian with Dugongidae, but its unreduced dentition indicates that it cannot be placed within Hydrodamalinae or Dugonginae. Thus by elimination its affinities rest with members of Halitheriinae, a taxonomic expedient embracing many ill-defined and oversplit taxa of non-hydrodamaline, non-dugongine dugongids. Domning and Thomas (1987) have attempted to sort out the phylogenetic relationships of selected Old World halitheriines, but the precise affinities of the New World members of this group continue to be problematic (Reinhart, 1976; Muizon and Domning, 1985). Our purpose here is not to provide a detailed systematic revision of this assemblage (which is now being undertaken by Domning [1988; personal commun.]), but instead to give a reasoned argument for the

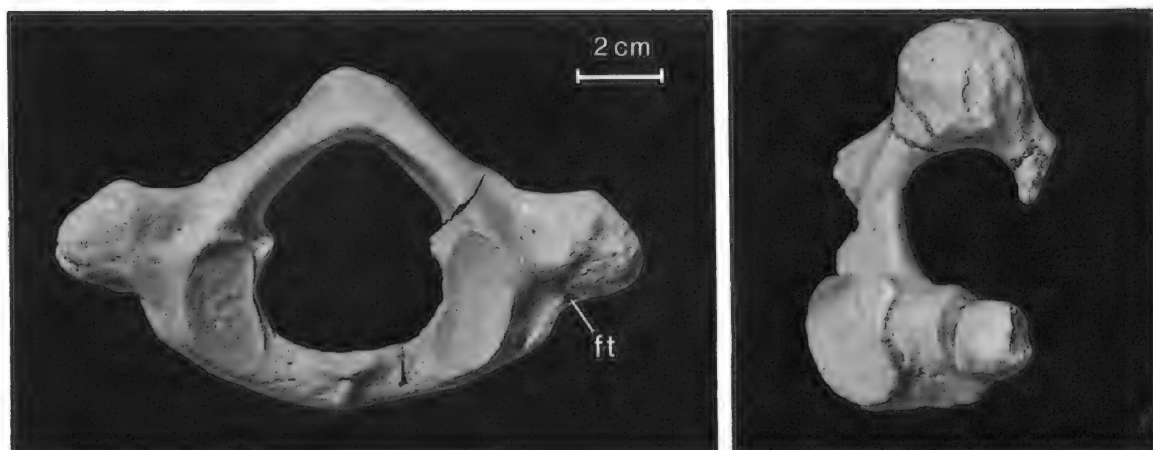


Fig. 8. Cervical vertebrae of sirenian axial skeleton (AMNH-VP 125781) referred to *Metaxytherium*, cf. *M. calvertense*. Left, atlas, anterior view; right, axis, anterior view.

identity of the Miranda material described above.

The Miranda jaw differs from that of *Dioptlotherium allisoni* of ?Early to Middle Miocene rocks of the eastern North Pacific (Domning, 1978) in having a more rectangular m3 and a shorter posterior root that does not impinge on the mandibular canal. "*Halitherium*" *olseni* (Reinhart, 1976), from the Early Miocene of Florida and now under study by Domning (personal commun.), is most readily distinguished from the Miranda form by the much smaller size of its teeth (although both share a trilobate m3).

By contrast, in gnathic features AMNH-VP 125780 closely resembles species of the extremely widespread Neogene genus *Metaxytherium* (table 3). According to Barnes et al. (1985), there were probably only two species of *Metaxytherium* in the New world—*M. calvertense* and *floridanum*—although many other supposedly distinct species have been named in the past. (Another Caribbean representative of this genus, *M. riveroi* [Varona, 1972] from the Middle Miocene of Cuba, is likely synonymous with *M. calvertense* [Muizon and Domning, 1985].) These two species can be distinguished on the basis of a greater rostral deflection of the jaw and deeper mandibular corpus in *M. floridanum* (Muizon and Domning, 1985). The minimum vertical depth of the mandibular corpus of AMNH-VP 125780 (63 mm) corresponds well with that of the type of *M. calvertense*

(65 mm). The heavily worn m3 of AMNH-VP 125780 appears to be metrically smaller than the unerupted m3 of the immature Peruvian specimen measured by Muizon and Domning (1985). However, to the degree that these teeth can be usefully compared, they seem to be very similar in shape and we attribute any differences in metrical values to wear, individual variation, or the method of measurement. The close morphological correspondence of the Maryland, Peruvian, and Puerto Rican forms in virtually all morphological details warrants their allocation to the same genus and probably to the same species.

As already noted, the Miranda axial skeleton (AMNH-VP 125781) is very similar to that of metaxytheres. It may additionally be noted that, for comparable measurements of homologous elements, AMNH-VP 125781 is 25–30% larger than "*Halitherium*" *olseni* (cf. Reinhart, 1976). A distinctive difference is the much less prominently developed and more ventrally placed transverse processes of the atlas in the Miranda form.

The only other issue connected with the allocation of the Miranda specimens to *M. calvertense* concerns the temporal range of this species. According to Monroe (1980), the Miranda Sand Mbr of the Cibao Fm was probably laid down very early in the Miocene, perhaps close to the Oligo-Miocene boundary (see Catalog). However, recent systematic studies made by Domning (1988) indicate that *M. calvertense* evolved—perhaps



Fig. 9. Unreferred small sirenian thoracic vertebra (AMNH-VP 125782) from AMNH loc. PR 87-4. **Top**, anterior; **bottom**, posterior.

from *M. krahuletzii*—during the Hemingfordian (late Early Miocene). The age of the Montera Fm, which yielded the Peruvian specimens described by Muizon and Domning (1985), is also somewhat uncertain (Early or Middle Miocene). For the present, the simple solution is to report the Miranda sirenian as *Metaxytherium*, cf. *M. calvertense*, to reflect the fact that it is possibly but not certainly a very early member of this species.

Small Miranda Sirenian

REFERRED MATERIAL: The presence of a second sirenian in the northeastern Caribbean during Miocene time is signaled by other finds from the Miranda Sand at locality PR 87-4, a diminutive thoracic vertebra and incomplete rib. The former specimen (AMNH-VP 125782) is a partial anterior thoracic (?T2), lacking the tips of the transverse and spinous processes and a substantial

portion of the centrum (fig. 9). However, it is possible to tell from the remaining part of the centrum's anterior articular surface that its epiphysis was completely fused, indicating that the specimen came from an adult animal. Small anterior demifacets are discernible on the upper part of the centrum, but no posterior demifacets can be detected. The centrum is seamlessly fused to the neural arch, and the spinous process is strongly inclined posteriorly. The vertebral canal is subcircular, save anteriorly where it is indented by a low keel on the posterior aspect of the centrum. The height and width of the canal are each approximately 17 mm. At present the greatest intertransverse width of the specimen is 72 mm; we estimate that this is within 10–15 mm of the original width. The prezygapophyseal facets are nearly horizontal and deeply set on the neural arches, so that their posterior margins seem to be surrounded by cuffs of bone. The postzygapophyseal facets are shallowly concave and slightly inclined.

Placement of the unassociated rib (AMNH-VP 125783) with the vertebra described above is provisional. Both ends of this specimen are missing, and we cannot infer where it may have been situated in the rib series. (If its position was at the caudal end of the series, it may simply be a terminal rib of *Metaxytherium*.) We estimate that its total length did not exceed 20 cm. Its maximum diameter is 2.3 cm.

COMPARISONS AND DISCUSSION: AMNH-VP 125782 grossly resembles anterior thoracics of other Neogene sirenians, and we have no doubts about its ordinal placement. What is unusual is its size: it is as small as or smaller than equivalent elements of Eocene sirenians, and approximately half the size of those of comparable anterior thoracics of *Metaxytherium* and most other later Cenozoic dugongids and manatees (cf. Domning et al., 1982). AMNH-VP 125782 is approximately 20 percent smaller than the second thoracic of *Caribosiren* described by Reinhart (1959) and is also considerably smaller than any of the thoracic vertebrae in the Rabell collection (see next section). AMNH-VP 125782 is therefore not likely to represent *Caribosiren*. The rib fragment also appears to be too small for assignment to this genus. The only Neogene form in the apparent size range of these

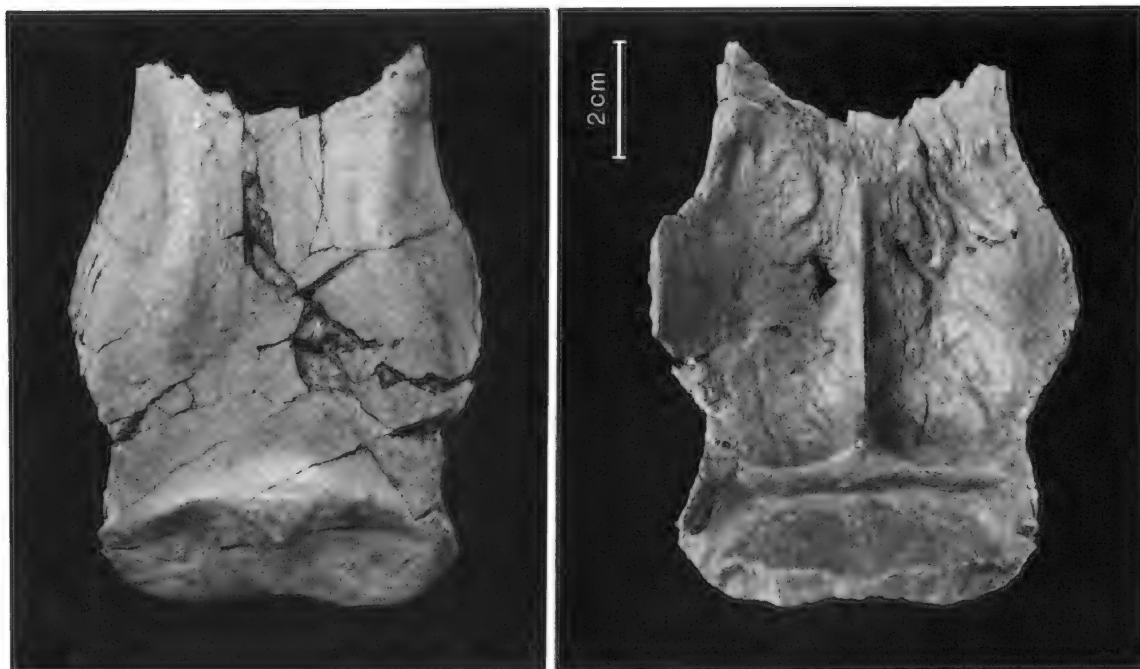


Fig. 10. Sirenian skull cap (AMNH-VP 125784) from Rabell Collection, possibly referable to *Caribosiren turneri*. Left, ectocranial; right, endocranial.

specimens may be the undescribed sirenian from the western Atlantic briefly mentioned by Barnes et al. (1985). Although AMNH-VP 125782 and 125783 probably represent a heretofore unknown sirenian taxon, in view of the inadequacy of the material available for diagnosis we shall simply refer to it as the "small Miranda sirenian."

Other Sirenian Remains

Sirenian remains were also collected during 1987 and 1988 at AMNH loc. PR 87-1, 87-2, 87-3, and 88-1. All of the fossils recovered at these sites are very fragmentary and cannot be allocated to specific taxa. Geological context and other pertinent information on these finds is presented under the appropriate formational and locality headings in the catalog.

The Rabell collection includes a large number of sirenian elements. Although their precise provenances are no longer known, it is probable that all of them came from exposures of the San Sebastian and Lares Fms in northwestern Puerto Rico (see Catalog). It is also likely that the majority of specimens belong to *Caribosiren turneri*, the only de-

scribed Oligocene sirenian from northern Puerto Rico. However, some specimens appear to relate to a second, larger form whose identity is not presently known.

SKULL: Unfortunately, there are no longer any sirenian teeth or jaws in the Rabell collection. There definitely were some, since Rabell's (ms.) display catalog mentions two lower jaws. In any case, this material cannot be presently located. There are, however, two skull caps (AMNH-VP 125784, 125785) in the existing collection that in size and morphology closely match the equivalent part of the holotype skull of *C. turneri* (UCMP 38722).

The skull caps are similar and may be described together (the better of the two, AMNH-VP 125784, is illustrated in fig. 10). Each consists of parts of the parietals and the supraoccipital, all firmly co-ossified in the manner typical for sirenians (Reinhart, 1976). The most prominent features of these specimens are the temporal and nuchal crests. The temporal crests are low, rounded eminences that progressively fade anteriorly without converging, which probably rules out their allocation to *Halitherium* (but see Reinhart, 1976). The nuchal crest supports a large,

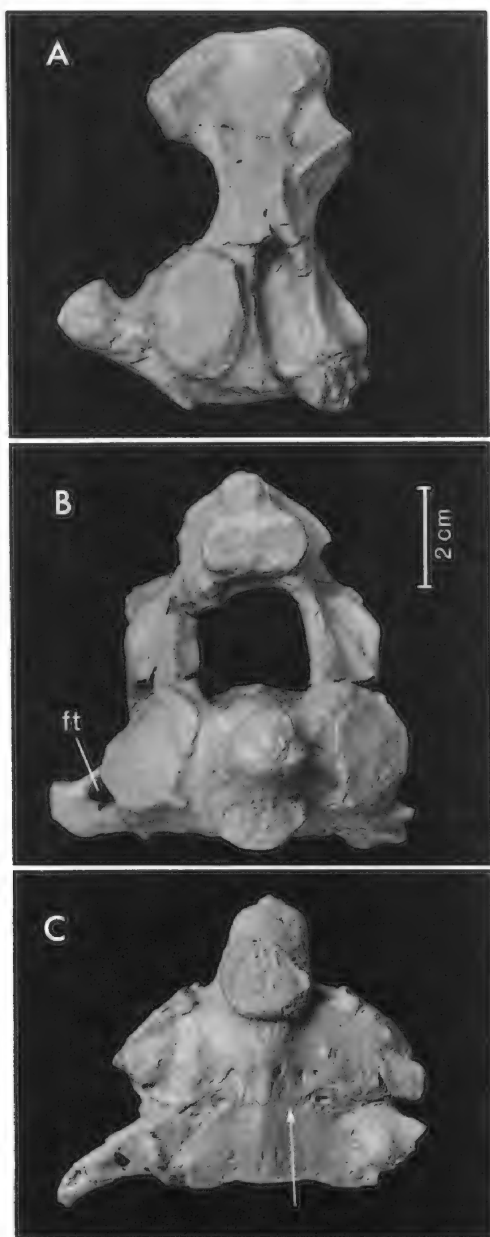


Fig. 11. Sirenian C2-C3 (AMNH-VP 125786) from Rabell Collection, possibly referable to *Caribosiren turneri*. A, lateral; B, anterior; C, ventral. The two elements are completely ankylosed—a rare anomaly in sirenians, not previously reported for halitheriines (arrow points to line of fusion).

triangular external occipital protuberance. The distance between the external occipital protuberance and the anterior border of the parietals, measured in the midsagittal plane, is approximately 70 mm in AMNH-VP

125784. The equivalent distance on UCMF 38722 is 61 mm (cf. Reinhart, 1959: 13, fig. 2). The biparietal width is 50 mm in AMNH-VP 125785, and 56 mm in AMNH-VP 125784.

RIBS AND VERTEBRAL COLUMN: Twenty-one sirenian ribs are contained in the Rabell collection. These can be divided into two lots on the basis of size and color. The smaller ribs all share a characteristic dark gray to brown coloration, and include the two specimens figured, described, and referred to *Caribosiren* by Reinhart (1959: 14, fig. 3). The three larger specimens are much more robust and much lighter in color than the ribs attributed to *Caribosiren*.

The most complete vertebrae in the Rabell collection are an axis and third cervical (AMNH-VP 125786) that are solidly ankylosed at their centra, articulations, and neural arches (fig. 11). The odontoid process of the C2 is long, blunt, and canted slightly dorsally. Its anterior articular facets are roughly circular and measure 25 mm in diameter. The left incisura transversaria of the axis is open dorsally. Other measurements of the axis are: tip of odontoid process to base of C2 centrum (as defined by suture remnants), 44 mm; ventral surface of centrum to dorsal surface of neural arch, 73 mm; diameter of vertebral canal, 22 mm.

The passageway for the vertebral artery is a complete foramen on C3; the bridge of bone defining the foramen dorsally is about one-quarter the thickness of the bridge that defines it ventrally. The posterior articular surface of the centrum is broadly concave and wider (42 mm) than high (23 mm). The postzygapophyseal facets are oriented obliquely, and face ventrally and posterolaterally. The distance between the internal margins of the two facets is 25 mm. The maximum width across the transverse processes can be securely estimated to have been approximately 80 mm.

The holotype material of *Caribosiren turneri* does not include any cervical vertebrae (Reinhart, 1959), but the size of AMNH-VP 125786 does not negate a relationship to that species. No other examples of the fusion of the second and third cervicals are known for halitheriines (cf. Kellogg, 1966; Reinhart, 1976), although this anomaly has been en-

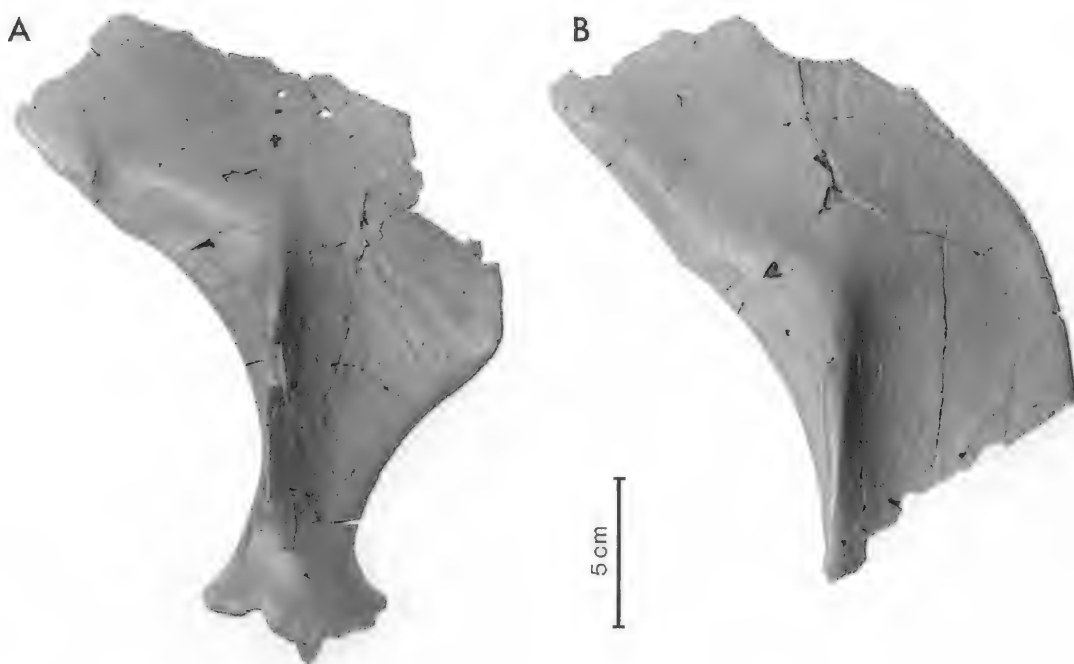


Fig. 12. Sirenian scapulae from Rabell Collection. A, AMNH 125787, right scapula, dorsal surface; B, AMNH-VP 125788, left scapula, dorsal surface (reversed to facilitate comparison).

countered in other dugongids and in trichechids (D. P. Domning, personal commun.). If these elements actually belong to the Puerto Rican species, *Cariborsiren* may now be additionally characterized by this unusual spinal autapomorphy.

Approximately 60 other vertebral elements are represented in the Rabell collection, but most consist of isolated centra and broken arches. Like the ribs, the few relatively complete specimens seem to be divisible into two classes which differ in size and coloration. Larger specimens are light in color, suggesting deposition in a carbonate-rich environment; the smaller ones tend to be darker, suggesting that they came from a shale or fine-grained sandstone. The close correspondence in size between some of the elements ascribed to *Cariborsiren* by Reinhart (1959) and the smaller Rabell specimens (including the fused C2–C3) reasonably assures that all belong to the same taxon. For the present the larger Rabell specimens will have to remain unallocated.

OTHER MATERIAL: There are two incomplete scapulae (AMNH-VP 125787, 125788)

in the Rabell collection that differ in size, preservation, and morphological details. Of the two, the right scapula (AMNH-VP 125787; fig. 12, left) is the more complete. Most of the specimen's vertebral border and portions of the spine and supraspinous fossa are missing. The blade is extremely broad (maximum anteroposterior dimension, 180 mm). The scapular spine is 95 mm in length and strongly inclined posteriorly. The axillary and upper (cranial) borders are deeply concave; the latter bears a moundlike swelling, presumably for muscle attachment. The scapular blade rapidly tapers laterally to form a neck that measures 35 mm at its narrowest point. The glenoid fossa is deep and measures 41 mm anteroposteriorly and 32 mm medio-laterally.

The left scapula (AMNH-VP 125788; fig. 12, right) lacks the margin of the vertebral border and the neck, acromion, and glenoid regions. Nevertheless, enough remains to indicate that it significantly differs from AMNH-VP 125787. The left scapula is about one-third larger but much less anteroposteriorly elongate than the right. Its upper border

is much less concave in profile and the prominence on the cranial border is more ventrally placed and less prominent.

OTHER OLIGOCENE AND MIOCENE VERTEBRATES FROM PUERTO RICO

Other Oligo-Miocene vertebrates known from Puerto Rico include chelonians, crocodilians, teleosts, and selachians. Eugene Gaffney and Peter Meylan (personal commun.) are currently studying turtle material from various sites in Puerto Rico, and it is likely that a number of important additions to the fossil chelonian fauna of the island will be made in the next few years.

At present the only published Oligocene turtle is the unnamed and fragmentary pelomedusid shell described by Wood (1972). The shell (AMNH-VP 1836) apparently came from an exposure somewhere along the road (now Highway 111) between San Sebastián and Lares (see Catalog). Williams (1989) and Meylan have reexamined this fossil and concur that it is an unknown pelomedusid. The question whether this was a marine or freshwater chelonian remains unresolved (Williams, 1989).

We have briefly surveyed the nonmammalian vertebrate fossils in the Rabell collection. Although a number of shark teeth, teleost vertebrae, and crocodilian bones are present, the best represented group is Chelonia. Included in the collection are a well-preserved pleurodiran cervical vertebra (AMNH-VP 24514), the proximal half of a chelonian femur, and more than a dozen large carapace and plastron fragments bearing buttresses and sutural areas. It is not known whether any of this material is referable to Wood's (1972) unnamed pleurodiran.

A comparatively large number of chelonian remains were recovered at PR 87-4, in the same Miranda Sand deposit that yielded the sirenian fossils described above. The preservation of this material is exceptional, and further work at this site would be very desirable. The best fossil recovered in the 1987 season was a nearly complete pleurodiran shell (AMNH-VP 24400), approximately 1 m in length (fig. 4C). Other elements recovered include a pleurodiran proximal humerus (AMNH-VP 24553) and pubis, and a

number of smaller shell fragments. Poorly preserved long bones and shell fragments were also recovered at PR 88-1.

CATALOG OF TERTIARY VERTEBRATE LOCALITIES

The purpose of this catalog is to list, in one place, all of the published and unpublished Puerto Rican vertebrate localities definitely of Tertiary age known to us. (A complementary partial list of Quaternary localities has been published by Pregill [1981b].) Localities are listed under the major geological unit in which they are situated, from oldest to youngest, insofar as this can be determined (see also figs. 2, 3). For a comparatively small island, the middle Tertiary rock fabrics of Puerto Rico are surprisingly varied; this has led to the recognition of numerous penecontemporaneous formations and members, which complicates the problem of arranging localities along a time line. Allocation of fossils to formal epochal subdivisions is mainly based on Monroe's (1980) evaluations of the ages of corresponding rock series. Because of continuing difficulties with the temporal correlation of Cenozoic deposits of northern and southern Puerto Rico (cf. Monroe, 1980), sites in the north and south are listed separately.

Formal formational names are considered to be English nouns and therefore Spanish accent marks (if any) are omitted. They are retained in other cases: thus San Sebastian Formation, but San Sebastián (town); Río Culebrinas Group, but Río Culebrinas (river).

Localities are usually fixed by reference to the rectangular-grid (XY) coordinate system used on most USGS 7.5' quadrangle maps of Puerto Rico.⁴ The numbers cited are in meters east and north of an arbitrary origin to

⁴ The Y benchmarks on the San Sebastián quadrangle map are incorrect. The upper benchmark (at top right-hand side of map) should read "58,000," not "60,000." The lower (at bottom left) should read "48,000," not "46,000." For the sake of convenience, Y coordinates for localities on the San Sebastián quadrangle have been measured from the printed 60,000 m benchmark. These values are placed in quotations; corrected values follow, in brackets.

the south of Mona Island. Grid coordinates are, of course, only approximate in cases where authors or sources have not provided sufficient indication of precise locations. The grid is not used on some recently published USGS maps, and localities lying within these quadrangles have been fixed by latitude and longitude.

OLIGOCENE AND MIOCENE
VERTEBRATE LOCALITIES OF
SOUTHERN PUERTO RICO
Juana Diaz Formation

The Juana Diaz Fm is a heterogeneous assemblage defined to include "all terrigenous beds, limestone, and chalk above the rocks of Cretaceous to Eocene age and below the unconformity at the base of the Ponce Limestone" (Monroe, 1980: 67). The formation is divided into "typical clastic beds," a limestone member, and an upper clastic member. The lower clastic strata of conglomerates and mudstones ("detrital unit" of Krushensky and Monroe, 1975) are dated to Early Oligocene by Moussa and Seiglie (1970). The limestone member may be Early Miocene, and the upper clastic beds are later still (?Middle Miocene). This would make the Juana Diaz time-equivalent to all of the San Sebastian, Lares, and probably the Cibao of northern Puerto Rico.

Petrified wood is apparently common enough in the basal beds of Juana Diaz to have warranted special mention in the first geological report on rocks of this formation (Berkey, 1915; Zapp et al., 1948). Mitchell (1922: 289) inferred that the "sandy character of the marly and shaly limestone and the presence of many fragmental fossils and plant remains indicate shallow-water deposition." The basal part of the lower clastic unit is primarily composed of boulders, cobbles, and breccias of volcanic rocks plus coral fragments in a detritus matrix. To Monroe (1980), this implied a shallow bay or beach environment in which streams discharged their contents into alluvial fans that were thereafter reworked by wave action (Monroe, 1980). However, in these same deposits, Moussa and Seiglie (1970) found that planktonic foraminifers, characteristic of deep-water oceanic environments, were common. Monroe (1980)

tried to resolve the discrepancy between depositional indicators by inferring that during early Juana Diaz time, the land must have been rapidly rising (promoting massive erosion on land) while the sea floor was rapidly dropping (creating deep-water conditions close to shore).

More recently, Fourcade and Butterlin (1988) furnished many examples of such mixed faunas in carbonates recovered from the Bahamas in Leg 101 of the Ocean Drilling Program. Specifically, they inferred that turbidites and debris flows must have been responsible for the transport of large shallow-water benthic foraminifers into sediments bearing planktonic forms. From correlation studies, they concluded that the redeposition of larger foraminifers in sediments of the same or similar age could be linked to sea-level changes; the reworking of older, larger foraminifers into different-age sediments seems to be related to tectonic events. Thus larger foraminifers in mixed-fauna contexts supply paleoecological information about original source areas, but not necessarily about the deposits in which they are intrusive.

In any case, the lithology of the basal Juana Diaz and the nature of its high-relief depositional contact with older rocks is further evidence that ancestral Puerto Rico was sub-aerial at the beginning of the Oligocene (cf. San Sebastian Fm).

1. Río Jacaguas (USGS Map I-863, Ponce quadrangle [Krushensky and Monroe, 1975]; X = 143,900, Y = 25,850).

Material collected and age: Partial lower jaw (holotype of ?*Halitherium antillense* [Matthew, 1916]), found with two fragmentary vertebrae and ribs. Early Oligocene.

Context and discussion: The fossils described by Matthew (1916: 25) were recovered from a "[s]hale bluff, west bank Jacagnas [sic] River, 1 km north, 1 km west of Juana Diaz, Porto Rico." This information places the collecting locality near the community of Las Lomas. In this area, the Eocene Guayo Fm abuts the lower clastic unit of the Oligo-Miocene Juana Diaz Fm along the San Patricio Fault (Krushensky and Monroe, 1975). Although both of these formations are exposed in the west bank of the Río Jacaguas,

the Guayo can be excluded as the source of the fossils because it is largely an epiclastic volcanic conglomerate. By contrast, the lower clastic unit of the Juana Diaz is predominantly a light blue-grey, calcareous, stratified sandy clay, exposed in bluffs 10–15 m high along the river (Monroe, 1980). As noted, this unit is usually interpreted as Early Oligocene in age on the basis of foraminiferal content (Moussa and Seiglie, 1970), which would make part or all of it older than the basal part of the San Sebastian Fm of northern Puerto Rico.

Reinhart (1976: 237) stated that Matthew's (1916) queried allocation of the Río Jacaguas fossils to *Halitherium* may be correct on the basis of tooth-locus count, but noted that *?H. antillense* "might equally well be synonymous with *Caribosiren* . . . , which was collected in the same general locality in undoubted Middle Oligocene strata." This reference to *Caribosiren* is puzzling, because as far as we have been able to determine, no sirenian remains from southern Puerto Rico have been assigned to this taxon. Perhaps "locality" is a lapsus for "lithology," in which case Reinhart's reference is to *Caribosiren* fossils from the San Sebastian Fm.

2. Howard University 1982-1 (USGS topographic map, Guanica quadrangle; X = 104,000, Y = 16,000).

Material collected and age: Sirenian vertebrae and ribs. Early Oligocene.

Context and discussion: "A large exposure on a N-facing slope S of La Luna, NE of Guanica. At least [30 m] of S-dipping limestones, sandstones, siltstones, and conglomerates are exposed; . . . sirenian vertebra [came] from a shell bed about halfway up the section. About [300–500 m] to the east, a similar exposure . . . produced several vertebrae and ribs from conglomerates near the middle of the exposed section. These are all mapped as the 'typical clastic beds' of the Juana Diaz Formation" (Daryl P. Domning, personal commun.).

These fossils appear to be equivalent in age to the ones from Río Jacaguas. No allocation is suggested by Domning.

3. AMNH PR 88-3 (USGS Map I-1042; X = 135,500; Y = 25,000).

Material collected and age: Chelonian shell fragments. ?Middle Miocene.

Context and discussion: This locality is situated in the only outcropping of the Upper Clastic Beds of the Juana Diaz Fm so far recognized. They are described by Monroe (1980: 73) as deposits within channels cut into limestones of earlier Juana Diaz age, and "consist largely of crossbedded sand and gravel and carbonaceous sand and clay." This suggests nearshore deposition, although Moussa and Seiglie (1970) claimed that the planktonic foraminifera indicate a deep-water marine context of deposition.

AMNH loc. PR 88-3 is situated in exposures of variegated, loosely consolidated quartzitic sands. The chelonian shell fragments, too small for identification, were found on the float at the side of the road that winds to the top of the hill being quarried by the PRCC (see entry under Ponce Limestone). We agree with Monroe that, lithologically, the upper clastic beds appear to reflect nearshore deposition.

Ponce Limestone

The Ponce Limestone is a comparatively pure, white to yellow limestone which formed as a shallow-water fringing reef off southern ancestral Puerto Rico. It lies unconformably on Juana Diaz rocks; estimates of its age range from Early Miocene to latest Miocene (Monroe, 1980). Bermúdez and Seiglie (1970) have correlated the Ponce ostracod fauna with the *Globorotalia margaritae* biochronozone (N 18-19), most of which is thought to be Early Pliocene (Berggren et al., 1985). We note that this interpretation, which is followed in figure 3, apparently requires a depositional hiatus in the south equivalent to all or nearly all of Aguada and Aymamon time. No vertebrate fossils have been reported from the penecontemporaneous Guanajibo Fm, very little of which is exposed.

1. Puerto Rico Cement Company (USGS Map I-1042, Peñuelas and Punta Cuchara quadrangles [Krushensky and Monroe, 1978]; X = 131,000, Y = 21,030).

Material collected and age: Sirenian ribs. Latest Miocene or Early Pliocene.

Context and discussion: Cooke (unpubl.

observ. cited by Monroe, 1980: 78) found some sirenian ribs in Ponce Limestone. The location of the sirenian site is not mentioned, although it is apparently situated in the PRCC quarry "near the top of the hill" on the west side of Ponce. (AMNH loc. PR 88-2 is situated on the same hill, but at a lower elevation.) No other information is available.

OLIGOCENE AND MIOCENE
VERTEBRATE LOCALITIES OF
NORTHERN PUERTO RICO
San Sebastian Formation

The San Sebastian Fm is the oldest in the northern carbonate sequence, and historically the most important formation on the island in terms of fossil vertebrate recovery. Opinion has varied as to whether this formation is exclusively Oligocene (Monroe, 1980). Bold's (1965, 1970, 1971) data indicate that the fossiliferous upper portions of the San Sebastian are Late Oligocene. Turner (1972) surmised that the lowest, mostly non-fossiliferous horizons were deposited in the medial Oligocene (= Late Oligocene in a two-division framework). Although there is evidence for Early Oligocene deposition in southern Puerto Rico (see Juana Diaz Fm), at present there is no basis for inferring that the basal part of the San Sebastian was laid down prior to the end of the Rupelian, and we shall assume that all of it is Late Oligocene.

The formation (fig. 4D) consists mainly of variegated clays, with marly clays and impure limestones at top that pass conformably into Lares Limestone. The basal units of the San Sebastian overlie the deeply weathered uppermost portion of the Middle Eocene Rio Culebrinas Group of the Older Complex, and are separated from the latter by a sharp, angular unconformity. These units include coarse conglomerates as well as fine-grained kaolinized clays derived from Rio Culebrinas rocks. Greenish- and grayish-tan silts and clays with a few, very impure, limestone horizons comprise the uppermost units.

The lithology of the San Sebastian is of considerable interest from the standpoint of depositional regimes. In lower units, iron oxides in the oxidized state predominate in heavily weathered clays. Higher in the sec-

tion, clays are less kaolinized and iron is found in the reduced state. Brackish-water marine fossils are common in the upper two-thirds of the section, but not in the lower one-third. Turner (1972: 36) argued that this sequence implies a progressive change in depositional regime, from terrestrial-fluvial to near-shore lagoonal to shallow-water marine.

The deeply weathered condition of Rio Culebrinas rocks and the high degree of local relief on the unconformity (~250 m; Monroe, 1973) indicate that ancestral Puerto Rico existed after middle Eocene time. Younger Complex deposits were progressively laid down on the seaboard side of this land mass. The San Sebastian Fm was not deposited at places where relief surpassed ambient sea level; in those locations, Lares rocks lie directly on the basement (Monroe, 1976). The basal beds in the vicinity of San Sebastián town are stratigraphically the lowest in the formation (Turner, 1972), and for this reason most of our collecting efforts were concentrated in this area.

It is not known which of the major drops in Eocene sea level charted by Haq et al. (1987) can be correlated with the period of erosion prior to the deposition of the basal San Sebastian in the north and the Juana Diaz in the south. Sea level rose dramatically during the Early Oligocene, which could be correlated with the deposition of the Juana Diaz. However, the magnitude of the Late Eocene drops is considerably smaller than the one which occurred at 30 Ma, on the boundary between the Early and Late Oligocene. According to Haq et al. (1987), global sea level was reduced by 160 m and remained comparatively low (relative to earlier levels in the Paleogene) until the start of the Miocene about 25 Ma (but see Matthews, 1988). This suggests that the increasingly marine aspect of the upper San Sebastian Fm was related to recovering sea level.

It is convenient to note here that, with the possible exception of UCMP loc. V-4852, no vertebrate fossils have been reported from the overlying Lares Lm. Lares rocks (as defined by Monroe, 1980) are relatively pure limestones that were deposited in clear water across much of the north-central San Sebastian landscape in the late Oligocene and early Miocene (Bold, 1971; Seiglie and Moussa, 1984).

The precise locations of Rabell's vertebrate localities are not known. Information on the Quebrada Collazo and Río Guatemala, two areas in which Rabell is known to have collected, is included under descriptions of AMNH loc. PR 87-1 and 87-3.

In 1987 and again in 1988 we attempted to prospect at every outcrop of San Sebastian deposits accessible from Highway 111, which runs almost without interruption over rocks of this formation from Moca to just west of Utuado—a distance of 35 km. We also surveyed many of the San Sebastian exposures between the Río Grande de Manatí and Bayamón.

1. AMNH PR 87-1 (USGS Map I-661, San Sebastián quadrangle [Tobisch and Turner, 1971]; X = 92,480; Y = "54,760" [56,760]).

Material collected and age: Sirenian vertebra. Late Oligocene.

Context and discussion: This site is located approximately 1.5 km NW of San Sebastián town plaza, on south bank of Río Guatemala 50 m immediately N of bridge for Highway 111.

The Río Guatemala is the principal river draining to the Río Culebrinas in the San Sebastián area. Units of the San Sebastian Fm are exposed along the lower part of its gorge. According to our informants, Rabell collected along the Río Guatemala, although it is not known whether he found any vertebrate fossils there. In 1987 we surveyed accessible parts of this river from the Lares cuesta to its union with the Río Culebrinas, but found only one productive site and one fossil, a sirenian lumbar vertebra (AMNH-VP 125789) recovered during initial prospecting of AMNH loc. PR 87-1. The element measures 120 mm in dorsoventral height (tip of spinous process to ventral surface of centrum) and approximately 210 mm mediolaterally (between tips of transverse processes). In size AMNH-VP 125789 matches the largest (?non-*Caribosiren*) vertebrae in the Rabell collection. Unfortunately, this section of the Río Guatemala was being dredged in 1988 in order to deepen the river's bed and thereby control erosion and flooding. The site is probably now deeply buried under river gravel.

The deposits at PR 87-1 consisted exclu-

sively of hard variegated clays containing small pebbles. In their texture and color characteristics they resembled the "mottled red and yellow clay" which Monroe (1980: 12) described as characteristic of units directly above the basal beds of the San Sebastian Fm. Invertebrate fossils were quite rare, which is also characteristic of the lower San Sebastian. It is not possible to be more precise than "Late Oligocene" in assigning an age for AMNH loc. PR 87-1. However, in the stratigraphic diagram accompanying the USGS San Sebastián quadrangle map (Tobisch and Turner, 1971), San Sebastian Fm exposures along the middle part of the Río Guatemala are shown as being stratigraphically lower than those near UCMP loc. V-4852 or in the upper gorge of Quebrada Collazo. This may indicate that AMNH loc. PR 87-1 is somewhat older than the other San Sebastian sites described here, in which case AMNH-VP 125789 would stand as the earliest known amniote fossil from Puerto Rico having a fixed locality.

Several hundred pounds of lag from the river's bank were screened in the hope that additional sirenian remains might be recovered. Unfortunately, screen washing yielded only a few fragmentary bivalve shells, echinoderm tests, and battered pieces of coral.

2. Howard University 1982-2 (USGS Map I-661, San Sebastián quadrangle; X = 92,500; Y = "54,300" [56,300]).

Material collected and age: Sirenian ribs. Late Oligocene.

Context and discussion: This site is described as a "large roadcut W of San Sebastian, on S side of Highway 111 [approximately 0.5 km] E of its intersection with Highway 446 . . . [R]ibs from a resistant, blocky, red and green variegated clay layer about three-fifths of the way up the cut. Above and below this layer are the typical brown and orange clays of the San Sebastian Formation" (Daryl P. Domning, personal commun.).

This site is close to AMNH loc. PR 87-1, but may sample a slightly higher stratigraphic level. Domning does not propose an allocation for the fossils.

3. AMNH PR 87-3 (USGS Map I-661, San Sebastián quadrangle; X = 96,580; Y = "53,100" [55,100]).

Material collected and age: Vertebrate bone fragment (?chelonian). Late Oligocene.

Context and discussion: Prospecting along the Quebrada Collazo was difficult and disappointing. From its headwaters the creek falls over the scarp of the Lares cuesta, a major physiographic feature which extends from San Sebastián to Corozal. The cuesta waterfall ("first waterfall") is almost immediately succeeded by two others ("second and third waterfalls") which cut through San Sebastian deposits; in total, the creek descends more than 75 m in less than a kilometer of horizontal distance. Access to the part of the creek between the second and third waterfalls is hampered by stands of dense tropical forest that extend all the way to the creek's gorge. This section of the Collazo is the most important paleobotanical collecting locality on the island (Hollick, 1928), having yielded numerous extremely well-preserved leaves and other plant parts. Since our informants indicated that Rabell repeatedly collected along this creek, we inferred that many of his vertebrate fossils must also have come from there. In 1987 we attempted to ascend the Collazo from its confluence with the Culebrinas, but were unable to climb the banks of the second waterfall from this direction. In 1988 we approached the second waterfall from Highway 111 and were able to get down into its gorge, and thus completed a survey of the entire channel. Although good exposures of San Sebastian clays were seen, especially in the gorges of the waterfalls, nothing of consequence was recovered. Only one vertebrate fossil was found, an unidentifiable ?chelonian long bone fragment from the lower course of the Collazo where it is crossed by an unnumbered road (the grid coordinates for PR 87-3 refer to this site). This was the only place in which we were able to screen, and it was highly unsatisfactory because by this point in its course the creek is generally less than 1 m in depth and its banks are very low.

We are puzzled by the apparent absence of sirenian fossils in the waterfall zone, since beautifully preserved plant remains were

found in abundance (implying close proximity to the coastline and therefore shallow waters at the time of deposition; see also Hollick, 1928). Other vertebrate paleontologists who have surveyed the Collazo in recent years have also ended up empty-handed (Domínguez, personal commun.). It is possible that Rabell retrieved vertebrate fossils from other parts of the hillside cut by the Collazo (cf. UCMP loc. V-4852). This would explain the presence of limestone matrix assumed to be of latest San Sebastian (or early Lares) lithology on certain bones in his collection. This interpretation could also apply to the fragmentary pelomedusid shell donated to the AMNH by Rabell in 1924, the provenance of which may be "limestone exposures along the main road from San Sebastian to Lares" (Wood, 1972: 2). However, it should be noted that other bones in the Rabell collection exhibit a shaly matrix residue, which is consistent with a Collazo provenance and the recollections of his workers.

4. AMNH PR 87-2 (USGS Map I-525, Bayaney quadrangle [Nelson and Tobisch, 1968]; X = 106,000, Y = 51,800).

Material collected and age: Unallocated sirenian rib fragments, teleost centra, and shark teeth. Late Oligocene.

Context and discussion: Very weathered fossils were recovered from the float on a cut bank facing Highway 129, directly N of latter's junction with Highway 111, NE of Lares town. Exposures at the cut are variegated sandstones mapped as undifferentiated San Sebastian Fm. Lignite is an important constituent of exposed deposits (cf. Hubbard, 1923), but no fossils were recovered therein.

5. University of California Museum of Paleontology V-4852 (USGS Map I-661, San Sebastián quadrangle; X = 99,800, Y = "51,520" [53,520]).

Material collected and age: Skull, lacking jugals and occipital region, with M2-3 in place, plus four thoracic vertebra (holotype of *Caribosiren turneri*). Probably latest Oligocene.

Context and discussion: Reinhart (1959: 8) described the location of this site, discovered by Mort Turner, as being "on road between

Sebastian [sic] and Lares, between BM. 348.2 m. and BM. 365.5 m. about 338 m. elevation, on side of hill in bluish to buff colored arenaceous limestone; abundant foraminifera and mollusca associated in same member."

Reinhart's (1959: 7, fig. 1) map shows the type locality of *Caribosiren* at a position that is now mapped as Lares Limestone on the most recent edition of the USGS San Sebastián quadrangle map. Uppermost San Sebastián units occur on the same hillside, but the closest outcrops are shown as 10–15 m downslope from UCMP loc. V-4852. Reinhart (1959: 15) noted that very few invertebrates were available for collection at this locality, and only one of them (the pelecypod *Lucina collazoensis*) is limited to the San Sebastián Fm. It is often difficult to separate uppermost San Sebastián from Lares in the field, because their contact is frequently gradational (Monroe, 1980). The San Sebastián unit exposed below the UCMP locality is described as a buff to dark-brown impure limestone on the quadrangle map, which correlates with Reinhart's description of the local rocks at UCMP loc. V-4852. This lithology occurs in restricted lenses and only at the top of the San Sebastián Fm as currently defined (Monroe, 1980). Where the *Caribosiren* locality is referred to the uppermost San Sebastián or transferred to the basal Lares makes little difference chronostratigraphically. Reinhart (1959) proposed a middle Oligocene date for UCMP loc. V-4852, but it is undoubtedly Upper Oligocene in the two-stage scheme now preferred for this epoch and is probably latest Oligocene in age.

Mucarabones Sand

The Mucarabones Sand consists of crossbedded, ferruginous, slightly calcareous sands with occasional limestone lenses, and is considered by Monroe (1980) to be the sediment deposited in the sea by several large paleorivers draining from eastern ancestral Puerto Rico. This formation was originally regarded as part of the uppermost San Sebastián Fm; it is now believed to be younger than San Sebastián, and is placed within the Puerto Rican Cenozoic sequence as the eastern lateral equivalent of the Lares Limestone and the lower two-thirds of the Cibao Fm

(Monroe, 1980). According to Monroe (1980), most of the formation appears to be Oligocene, although in the region of Bayamón it may be Miocene. If age determinations for the Lares made by Bold (1965, 1971) are accepted, most of the Mucarabones Sand is probably Early Miocene in age. If PR 87-5 is any guide, this formation is probably fairly fossiliferous and warrants additional work.

1. AMNH PR 87-5 (USGS Map I-508, Naranjito quadrangle [Pease, 1968]; X = 173,400, Y = 59,800).

Material collected and age: Sirenian bone fragments, possible ray jaw fragments, and shark teeth. Probably Early Miocene.

Context and discussion: This locality is 1 km WNW of the junction of Highways 819 and 861, or 0.5 km from the center of Piñas village, on land being cleared for the Laderas del Toa housing development. This area lies immediately to the west of the type area of the Mucarabones Sand as defined by Monroe (1980). Sandstones bearing vertebrate remains are mottled green in color and overlie redder sands. All material is fragmentary. Invertebrate shells are comparatively rare, but crustaceans (crabs) are not uncommon. These facts seem to bear out Monroe's (1980) interpretation that the Mucarabones is basically a nearshore deposit.

Cibao Formation

The Cibao Fm is lithologically variable to a high degree, being predominantly calcarenite in the central part of its areal exposure (Manatí quadrangle), marl-limestone-sand in its eastern parts, and gravelly in the west (Monroe, 1980). With the possible exception of the Guajataca Mbr (see below), other members of the Cibao (Montebello Limestone, Rio Indio Limestone, Almirante Sur Sand, and Quebrada Arenas Limestone) have not yielded vertebrate fossils to date. Monroe (1980) inferred from the occurrence of larger benthic foraminifers like *Lepidocyclus undosa* and *Heterostegina antillea* that the lower two-thirds of the Cibao is Upper Oligocene and the upper one-third is Lower Miocene. However, he did not attempt to deal with problems of reworking or redeposition that complicate correlation elsewhere in the Ca-

ribbean (Fourcade and Butterlin, 1988). Planktonic foraminiferal evidence reported by Bold (1965, 1971) tends to indicate that the Cibao is mostly or entirely post-Oligocene, and is most probably Early Miocene in age (especially if delimited as suggested by Seiglie and Moussa [1984]).

It is convenient to note here that there are no records of vertebrate fossils having been found in the superjacent Aguada, Aymamon, and Camuy. These formations are generally thought to be Middle to Late Miocene, although the Camuy may be partly Pliocene (wholly Pliocene, as redefined by Moussa et al., 1987). Their lithologies appear to record shallow-water conditions in Aguada time being succeeded by deeper water conditions during Aymamon time, during which the sea transgressed over the Aguada landscape. At the top of the Aymamon is an erosional unconformity which Monroe (1980) correlated with a significant marine regression caused by uplift in central Puerto Rico. Seiglie and Moussa (1984) attempted to correlate this unconformity with a global eustatic cycle, the regression representing sea level lowering either at the beginning of the Late Miocene (10 Ma) or at the start of the Pliocene (5 Ma).

1. AMNH PR 88-3 (USGS Map I-751, Bayamón quadrangle [Monroe, 1973]; X = 178,700; Y = 63,000).

Material collected and age: Chelonian remains and other vertebrate fossils. ?Early Miocene.

Context and discussion: Eugene Hartstein (personal commun.) collected vertebrate fossils from clayey facies on both sides of Highway 2 near the town of Hato Tejas. Turtle remains from one of these sites are presently being studied by Eugene Gaffney. Upper Cibao deposits are found on both sides of the highway (especially on the south side), where they are discontinuously overlain by great thicknesses of Aguada and Aymamon limestones. These limestones are comparatively pure and unlike the earthy limestone of the upper Cibao, which makes it highly probable that Hartstein collected his samples in rocks of the latter unit.

In 1988, we prospected in the areas recommended by Hartstein, but found only one site that may merit additional attention. A

high hill consisting of upper Cibao deposits and capped by Aguada limestone rises south of Highway 2. In sandy deposits on the eastern side of the hill we retrieved a few chelonian shell fragments. On the hill's south-eastern side there is a well-exposed 50 m scarp with a prominent lens (0.5 m) of lignite containing twigs and a few leaves. From the lignite we recovered a shark tooth and a probable teleost rib. This is the only lignitic zone known in upper Cibao deposits other than the one near Moca (see AMNH loc. PR 88-1). However, unlike in the latter, there are no gravelly channel deposits underlying the lignite.

Coordinates given above are those of the AMNH site; Hartstein's localities cannot be accurately fixed.

2. AMNH PR 87-4 (USGS Map I-473, Corozal quadrangle [Nelson, 1967]; 66°18'45"W, 18°22'21"N [map lacks grid]).

Material collected and age: Partial jaw with cheekteeth, partial axial skeleton, and other sirenian remains described earlier in this paper and reported as *Metaxytherium*, cf. *M. calvertense*; vertebra and rib of a smaller, unidentified sirenian; nearly complete pleurodiran shell; other shell and long bone fragments. Early Miocene.

Context and discussion: Monroe (1980) briefly noted the presence of sirenian bones in marly typical Upper Mbr limestone exposed on a hillside along Highway 820 west of Toa Alta. We recovered several fragmentary sirenian specimens (mostly ribs) from marly strata on the same hillside. More noteworthy was the discovery of well-preserved sirenian and chelonian remains in underlying Miranda Sand exposed at the same locality (fig. 4A, B). Our locality is slightly to the west of Monroe's, at a point 250 m ESE of the intersection of Highways 820, 677, and 678, and on the S side of Highway 820.

As exposed at PR 87-4, the Miranda Sand is a well-defined channel approximately 2–3 m thick and at least 50 m wide. The deposit consists of a well sorted, poorly consolidated, light green to tan sand unconformably overlying white, extremely indurated Quebrada Arenas limestone. Fossils were encountered at all stratigraphic levels within the sand horizon. One specimen, a partial sirenian rib,

was found incorporated into the top of the underlying limestone (probably the result of an episode of surficial solution and recrystallization of the relatively pure calcium carbonate in this member). Two oyster reefs, each approximately 30 cm thick, occur in the top meter of the sand. The partial jaw (AMNH-VP 125780) referred to *Metaxytherium*, cf. *M. calvertense* was found just above the higher oyster bed. Several other sirenian specimens found in the higher part of the section had been utilized as solid substrates for oyster holdfasts. The axial skeleton (AMNH-VP 125781) referred to the same species was found in the basal part of the section (fig. 4B). Although other small and isolated outcrops of Miranda Sand exist to the east and west of PR 87-4, no vertebrate fossils were found in them. Elsewhere in the immediate vicinity, earthy limestone of the upper Cibao rests directly on the Quebrada Arenas, with no Miranda Sand interposed—an indication of the latter's discontinuity.

According to Monroe (1980), the Miranda Sand Mbr of the Cibao Fm is a discontinuous channel deposit, maximally 10–20 m thick and composed of apparently fluvial sediments deposited near the seacoast by rivers. The sand contains no marine invertebrates and is noncalcareous. It cannot be Quaternary because the channel deposits cut into Quebrada Arenas limestone and are overlain by the Upper Mbr of the Cibao. Monroe (1980: 43) argued that the rivers which deposited these sands were rejuvenated by the uplifting of the central part of the Puerto Rican landmass in the terminal Oligocene. Uplift raised the newly deposited Quebrada Arenas limestone above sea level, permitting the rivers to cut trenches in which alluvium collected. Shortly thereafter, subsidence of the coastal shelf drowned the floodplains of these rivers, creating conditions which permitted the growth of oyster reefs like the one seen at PR 87-4. If this reconstruction is accurate, the Miranda fossils probably date from some time within the early part of the Early Miocene. Seiglie and Moussa (1984) suggested a definitely Miocene date for the deposition of the Quebrada Arenas, but were unable to resolve clear transgression-regression cycles in the Cibao. The new Vail curve (Haq et al., 1987) shows sea level drops at the beginning,

middle, and end of the Early Miocene (respectively 25, 21, and 16 Ma). Between these drops sea level rose markedly, although not to the levels characteristic of the Paleogene. Whether uplift or eustatic effects (or both) were responsible for rejuvenation of the Miranda river remains to be demonstrated.

3. AMNH PR 88-1 (USGS Map I-569, Aguadilla quadrangle [Monroe, 1969]; X = 76,700; Y = 63,300).

Material collected and age: Fragmentary chelonian, crocodilian, and sirenian remains; vertebrae of boid snake and ?iguanaid described earlier in this report. Early Miocene.

Context and discussion: This locality is situated on the north side of Highway 111, 0.4 km E of the intersection of the latter and (new) Highway 2. The area around the locality has been greatly modified for new construction. The hillside on which PR 88-1 is located has been carved back for about 50 m from the roadway, thereby creating a cliff face about 15–20 m high (fig. 4E). In the top 15 m of this face, a stratum of friable, earthy, slightly tilted limestone overlies a series of clays. One vertebrate fossil, a crocodilian vertebra (AMNH-VP 24499), was recovered from the latter facies. The bottom 1–5 m is composed of a series of sands containing variable amounts of ligneous material, gravels, and bone. The top of the hill has been partially leveled, but in unmodified areas Aguada Lm can be seen to surmount the earthy limestone.

The immediate vicinity of PR 88-1 is mapped as undifferentiated Cibao (Monroe, 1969). The only defined members of the Cibao which outcrop in westernmost Puerto Rico are the Guajataca Mbr, which notably contains large quantities of sand and gravel, and the Upper Mbr, which does not. Monroe (1980) attributed the origin of the interbedded gravels, sands, shales, and impure limestones of the Guajataca Mbr to the great northwestern river, which was still active in Cibao time. Nevertheless, at present we prefer to assign the material from PR 88-1 to the Upper Mbr. The limestones on the cliff resemble upper member lithology as described by Monroe (1980), and their position subjacent to Aguada rocks supports this interpretation. The lignitic sands may be a di-

agnostic marker: Monroe (1980: 39) recorded having seen only one lignite horizon in Cibao rocks, in an Upper Mbr facies at a place 6 km to the west of PR 88-1. The only other reasonable alternative is to interpret the unconformity between the limestones and gravelly sands as a contact between Guajataca and Upper Mbr facies. In that case, the fossiliferous horizons would be part of the uppermost Guajataca. In any event, because of considerable imprecision in the dating of Cibao rocks, choosing either alternative has little effect on the age estimate for the fossils. The basal Aguada contains invertebrates of early Middle Miocene age (Seiglie and Mousa, 1984); the fossil vertebrates of PR 88-1 are therefore no younger than this, and are probably best placed in the late Early Miocene.

Compositionally similar—but not identical—to the beds exposed at this locality are outcrops of limestone, chalk, and basal sands and gravels lying west of Highway 2 and extending out to Punta Higuero. Monroe (1980: 39) regarded these exposures as “apparently a western extension of the upper member.” Several of these were examined in 1988, but no vertebrate fossils were recovered.

The fossiliferous sands and gravels at PR 88-1 are thinly stratified, highly lenticular, and cross-bedded. The highest horizon within these deposits is notably ligneous and dark brown. Beneath this horizon is a loosely consolidated sand containing numerous small lenses (5–20 cm) of almost pure gray clay. Some ligneous material is found in this layer, including well-preserved leaves. The basal part of this layer becomes increasingly gravelly down-section. It is separated by a distinct unconformity from an exceptionally indurated series of thin laminae of cemented gravels and sands in which several thin oyster reefs occur. Fossil vertebrate remains were found in all layers, being rarest in the ligneous horizon and commonest in the sand with clay lenses and leaves (fig. 4F). Preservation varied greatly within horizons; most of the bones recovered were almost unrecognizable as such because they had been abraded into small ovoids.

The sands and gravels at PR 88-1 clearly represent a high-energy fluvial or beach environment. Although we provisionally place

the origin of these facies late in the Early Miocene, it could as easily be argued that they are time-equivalent to the ?earlier Miranda Sand outcrops in the central part of the island. This interpretation could be decisively favored on stratigraphic grounds if the fossiliferous sands rested on easily recognized Quebrada Arenas rocks, as at PR 87-4, but this member has not been recognized west of longitude 66°30'W (near Montebello).

Uncertain Formation

There are only two localities that warrant discussion under this heading. The first is not a paleontological site, but it has some related geological significance. The second is the unrellocated type site of the echimyd rodent, *Puertoricomys* (= *Proechimys*) *corozalus*.

1. Deposits of possible San Sebastian age in Barrio Calabazas. Barrio Calabazas, 3–4 km south of San Sebastián town, contains a number of thin, isolated exposures which are identified as “Quaternary high-terrace deposits” (QT_t) on the San Sebastián quadrangle map. These exposures overlie tuffs of the uppermost Rio Culebrinas Fm and are not directly connected to any mapped San Sebastian rocks. They consist of very weathered, variegated clays and therefore do not have the fresh appearance of typical Quaternary deposits in the general vicinity (e.g., floodplain of Río Guatemala). Turner (personal commun.) believes that some of these exposures are in fact Tertiary, and possibly San Sebastian in age. He found lignitic material, with some identifiable leaves, in one of them (X = 95,300, Y = 50,450) while conducting fieldwork in the late 1940s. If they are Tertiary, these exposures would have been closer inland to ancestral Puerto Rico than is the main band of sediments preserved somewhat further north. Although we confirm Turner’s assessment that some of these exposures probably antedate the Quaternary, it was difficult to explore them satisfactorily because of the large amount of residential construction in this area in the last 40 years. Turner’s locality was relocated, but the exposures he saw along fresh road cuts are now slumped and covered with foliage. No lignitic material or fossil leaves were found.

2. Corozal Limestone Quarry. This site yielded the holotype and only known specimen (a left mandible) of the echimyid *Puertoricomys* (= *Proechimys*) *corozalus* (Woods, 1989; see also Williams and Koopman, 1951) and some unallocated turtle and lizard bones. A label accompanying these bones, which were found in 1930 by James Thorp, specifies that they came from a "crevice in Corozal Limestone Quarry" (Williams and Koopman, 1951: 1). Williams and Koopman speculated that the material may be truly Pleistocene (or older), on the ground that neither the jaw nor the lizard bones appear to belong to any known Holocene taxa (see also Williams, 1989).

In order to fix the position and probable age of this locality, Clayton Ray attempted to relocate it in 1958 (full text quoted by Williams, 1989: 27):

... [W]e found only one active limestone quarry [near Corozal]. This quarry lies at the west side of town just north of route 159. ... An old unused quarry lies adjacent to this one, and another small unused one lies on the south side of town just beyond the Catholic college. One of these latter must have been the source of *Proechimys corozalus*. ... The active quarry ... looks like a good prospect for fissure material. ... [F]issures mainly with water worn walls and sometimes with drip stone deposits on walls filled with variable unconsolidated brown earth [were found]. A number of fissures observed terminated above abruptly at base of shale layers, suggesting that fissure filling may be very old but this is not certain as erosion of Quaternary caverns may have been controlled in part by insoluble shale strata.

No fossils were recovered by Ray. In 1988, we visited these quarries and were similarly unsuccessful. (The one near the Catholic college is no longer a recognizable physiographic feature; it has been filled in or covered over by new construction.) The quarry active in 1958, now the site of a small plant for fabricating cinder blocks, is mapped on the Corozal quadrangle at approximately 18°20' 45"N, 66°19'30"W. This places it on a small exposure of deeply weathered, brecciated limestone of Paleocene-Eocene age, known since Berkey's (1919) work as the Corozal Lm.

We caution that it is far from certain that the type site of *Puertoricomys* must be one of the quarries identified by Ray. The "Co-

roزال Limestone Quarry" named on the label may have been a quarry *into* limestone of Corozal Lm facies, as other workers appear to have assumed; on the other hand, it may also have been Thorp's gloss for a local quarrying operation. Easily mined, construction-grade limestone of Lares and Cibao facies outcrops widely in the Corozal quadrangle (Nelson, 1967), and such outcrops can be found less than 1 km north of the Corozal town plaza. The "crevice" which yielded *Puertoricomys* may in fact be located in these younger limestones. In this case the fissure fill could be no older than early Neogene, and possibly no older than Pliocene (i.e., subsequent to the marine transgression which marks the end of Camuy time and, presumably, the onset of the present karstification episode in northern Puerto Rico). Woods (1989) noted that, while this rodent deserves generic distinction, it is certainly heteropomyine in its immediate affinities. Since no additional material has been referred to the hypodigm of this rodent, nothing further can be said about its placement, either phyletically or stratigraphically.

SUMMARY

(1) Parts of the Greater Puerto Rican Shelf have been emergent, probably continuously, at least since the late Paleogene (end of the Middle Eocene, ca. 40 Ma). This is indicated geologically by the high-relief unconformity between Older Complex rocks and the basal formations of the carbonates on the north and south sides of the island. It is also indicated by the absence of post-Paleogene carbonates in the Cordillera Central Province. Still earlier emergences (e.g., volcanic piles that became subaerial during the Cretaceous) are not out of the question, although there are no useful data on this point.

(2) Conditions appropriate for the formation of a terrestrial biota existed at least as early as the Late Oligocene (30–25 Ma), because by that time ancestral Puerto Rico already supported a diversity of floral complexes (mangrove, upland-subtropical, and cool-temperate "communities" of Graham and Jarzen [1969]). Indeed, the diversity of these complexes (165 palynomorphs) is a strong indicator that terrestrial/coastal plants

were already long established prior to the Late Oligocene. Whether this ancient biota included a faunal component is not yet known; vertebrate fossils of correlated age consist of marine forms with the single exception of a pelomedusid turtle that may or may not have been freshwater.

(3) Chelonians, crocodilians, and sirenians inhabited shallow shelf waters off both the northern and southern coasts of ancestral Puerto Rico during the entire period for which there is now a Tertiary vertebrate fossil record (ca. 30–16 Ma). The vertebrate record is extremely poor for Middle Miocene through Pliocene time, although it is relevant to note that little paleontological prospecting has been undertaken in late Tertiary sediments of Puerto Rico.

(4) Presumptively terrestrial vertebrates—a boid and an ?iguanaid—first appear in the fossil record in contexts dated as Early Miocene. They correlate in age with at least some of the small vertebrates found in amber in Hispaniola, although no taxa are shared at low hierarchical levels. Lack of correlation at low hierarchical levels may be artifactual: ambers are unlikely to entrap large vertebrates, and coarse sediments in high-energy depositional contexts are unlikely to preserve very small ones. There are no terrestrial mammalian fossils of confirmed pre-Quaternary age.

(5) The recent discoveries discussed here are not, by themselves, sufficient to establish the comparative likelihood of vicariance vs. dispersion as the predominant mode of faunal formation in Puerto Rico and the rest of the West Indies. But they are a start in the right direction. Most investigators who have wrestled with the problem of mode have either ignored the possible contribution of paleontology or have relegated it to a subsidiary role (e.g., instantiating parsimony arguments based on the distribution of extant taxa). This is understandable, because for many groups (e.g., insects) it is unlikely that a fossil record of any significance can be recovered. For vertebrates, however, we think that the potential is somewhat greater. For this group, a good record could eventually prove to be crucial for testing biogeographical hypotheses, because the documents of paleontology—fossils—have a direct bearing on *which* taxa

(biota) occupied *which* land masses (space) at *which* point in earth history (time). However auspicious the configuration of Antillean landmasses might have been for colonization in the past, land animals either took advantage of smaller water barriers (or no water barriers) or they did not. Either they arrived *en bloc* as strict vicariance requires, or they managed their journeys separately as dispersionists contend. And nothing will be so compelling as fossil evidence as a means for choosing between these alternatives. Of course, the prospecting effort will be laborious; of course, the eventual paleontological record will be imperfect at some level; and, of course, agreement is never likely to be universal on what that record means. But the effort will be worthwhile if new avenues of insight into biogeographical processes are opened that cannot be achieved by other means.

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